EXPERIMENTAL STUDIES ON SPECIES RELATIONSHIPS IN *ERYTHRINA* (LEGUMINOSAE: PAPILIONOIDEAE)[1]

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ABSTRACT

Erythrina *L. comprises about 112 species distributed throughout the tropics and subtropics. Most species are trees or shrubs, and most are diploids with* n = *21. All are adapted to bird pollination, some by passerine birds and others by hummingbirds.* Erythrina *is subdivided into five subgenera and 27 sections. Research concentrated on sect.* Erythrina, *with 36 species centered in Mexico and Central America; selected species in other sections were also studied. Experimental interspecific hybridizations and self-compatibility trials were conducted using cultivated trees at several botanical gardens in Hawaii. Comparative morphological analyses were made of the hybrids and their parents. Studies of population structure and natural hybridization were carried out in natural populations of hummingbird-pollinated sect.* Erythrina. Erythrina *species are self-compatible, but some inbreeding depression is associated with selfing. Within sect.* Erythrina, *interspecific hybrids are obtained just as readily as are progeny from within-species outcrosses. The hybrids are vigorous, fertile, and by several measures exhibit interspecific heterosis. At greater taxonomic distances between the parental species (between sections and subgenera), crossability, viability, and fertility of the hybrid progeny are generally lower than in intrasectional hybridizations. Some hybrids were obtained between species of different subgenera indigenous to different continents. There are probably no absolute internal barriers to hybridization among all the diploid species of* Erythrina. *The genus may be characterized taxogenetically as a homogamic complex. Interspecific hybrids are intermediate between their parental species in morphological traits, including macroscopic features of the inflorescence and flower and microscopic features of the leaf epidermis. The inheritance of particular features of the male parent in the progeny allows for confirmation of hybridity. Species of sect.* Erythrina *are generally allopatric, but field studies of natural populations in southern Mexico revealed several localities where two species do occur sympatrically and where natural hybrids are found. Traplining hummingbirds, the pollinators of sect.* Erythrina, *are implicated as the agents of interspecific hybridization among sympatric species. The results of experimental hybridization, together with studies of comparative morphology and distribution patterns, suggest that some species of* Erythrina *are stabilized hybrid derivatives.*

Experimental hybridization studies have been a cornerstone of research in plant biosystematics since the emergence of this synthetic field. Much of the work of early biosystematists was directed toward efforts to define taxa and taxonomic categories on the basis of reproductive barriers as revealed by experiment, an approach exemplified by the studies of Clausen et al. (1939, 1940) and their proposal

[1] *This study was undertaken as part of a doctoral dissertation at Washington University, St. Louis, Missouri. Peter Raven first suggested the research on* Erythrina *biosystematics as a dissertation topic and helped in innumerable ways during the research. His ideas on plant evolution and the role of hybridization in the evolutionary process provided the conceptual framework upon which this study is based. Rupert Barneby and the late B. A. Krukoff introduced me to the the systematics of* Erythrina *and suggested relationships among the taxa of particular interest for the experimental studies. This work was made possible by the generous support of the three Hawaiian botanical gardens, and especially by the efforts of their respective directors and chief horticulturists: William Theobald and Scott Lucas at Pacific Tropical Botanical Garden; Keith Woolliams and Cecilia Ufano at Waimea Arboretum; and Paul Weissich and Daniel McGuire at Ho'omaluhia Botanic Garden. Gerald Carr at the University of Hawaii provided use of his cytological laboratory and excellent advice on the handling of chromosomes. Michael Veith provided assistance and advice with the scanning electron microscope at Washington University. Hiroshi Tobe prepared the leaf sections illustrated in Figures 19, 21, and 23. Conversations with and comments by Héctor Hernández and Peter Hoch helped to improve the manuscript. Alina Chacón and Mary Merello assisted in the preparation of the manuscript and figures. As a graduate student I was supported by fellowships from the Danforth Foundation, Washington University Division of Biology and Biomedical Sciences, and Missouri Botanical Garden. The research was funded by grants from the National Science Foundation (DEB 81-20386) and Elizabeth Neill.*

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ANN. MISSOURI BOT. GARD. 75: 886–969. 1988.

to establish ecotypes, ecospecies, coenospecies, and comparia as universal units of classification to replace the traditional ones. The criteria used to define taxa on the basis of fertility relationships and the enormous labor required to obtain the experimental results on a broad scale proved impractical for a general-purpose classification system, and most present-day biosystematists have rightly abandoned the earlier efforts to "meddle" with the traditional taxonomic hierarchy.

Experimental hybridization studies continue to play a central role in research on the nature of species relationships, however, and their usefulness extends far beyond the requirements of formal taxonomy. They provide the material for a broad spectrum of integrated studies in the genetics of evolutionary divergence. Research on long-lived perennials, although it requires patience and a long-term commitment of labor and resources, is particularly amenable to hybridization programs because the parentals and several generations of offspring can be grown side-by-side, and many comparative studies can be carried out with the living plants.

This paper describes the results of experimental investigations into the biosystematics and reproductive biology of *Erythrina* (Phaseoleae), a widespread genus comprising more than 110 species, most of them tropical trees. The research was concentrated on species of sect. *Erythrina*, a complex of 36 species centered in southern Mexico and Central America (Mesoamerica), but other taxa of *Erythrina* were included in some phases of the investigation. The results of the research are used to establish a series of hypotheses regarding species relationships and evolutionary history of *Erythrina*. The hypotheses are presented here in sequence: each is dependent on the validity of the previous hypotheses.

Hypothesis 1. The species of sect. *Erythrina* can all hybridize freely with each other, and the resulting hybrids are as fertile as the parents. The section is a homogamic complex, and internal, postmating isolating barriers between the species are absent.

Hypothesis 2. The interfertile homogamic complex encompassing sect. *Erythrina* extends, to a greater or lesser degree, to species in other sections and other subgenera of the genus. Any diploid *Erythrina* species can mate with any other to form a viable F_1 hybrid, but hybrids between widely divergent species may exhibit varying degrees of sterility. The genus as a whole may be characterized taxogenetically as a series of interfertile homogamic complexes with weak to moderate reproductive barriers between the complexes.

Hypothesis 3. The widely foraging hummingbirds that pollinate trees in sect. *Erythrina* ensure effective outcrossing even in the isolated populations of small neighborhood size and low density characteristic of these species. Self-compatibility and occasional autogamy allow establishment of a population from a single founder individual. When two species of sect. *Erythrina* are sympatric, the pollinating birds do not discriminate between them, and interspecific pollen transfer is likely.

Hypothesis 4. The species in sect. *Erythrina* are mostly restricted in geographic range and are usually allopatric, separated by habitat differences. For the most part, these factors are effective barriers to interspecific gene flow. However, sometimes different species do come into contact in nature, and then fertile hybrids are formed.

Hypothesis 5. Patterns of distribution and phenetic variation in sect. *Erythrina* indicate that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species. In the changing climates and dynamic geomorphologic landscape that have characterized Mesoamerica since the Miocene, and with the consequent migration of vegetation types and mixing of floristic elements, formerly allopatric species may have come into contact a number of times. With the temporary breakdown of external isolating barriers, the interfertile species hybridized, and the subsequent segregation and stabilization of hybrid derivatives has contributed to the proliferation of *Erythrina* species in Mesoamerica.

The first two hypotheses can be tested directly by experimental hybridization programs. The third and fourth can be substantially confirmed by observations of mating behavior and patterns of variation in natural populations. The fifth hypothesis is historical and can only be inferred by drawing on information obtained by testing the first four. The "level of confidence" (Gottlieb, 1972) in the final hypothesis of hybrid speciation in *Erythrina* is dependent upon the strength of the evidence presented in this paper in support of the four antecedent hypotheses.

This research was made possible by the existence of the extensive living collections of *Erythrina* at three botanical gardens in Hawaii: Pacific Tropical Botanical Garden in Lawai, Kauai; Waimea Arboretum in Haleiwa, Oahu; and Ho'omaluhia Botanic Garden in Kanehohe, Oahu. The cultivated *Erythrina* collections were assembled, beginning

in the early 1970s, through the efforts of the *Erythrina* monographer B. A. Krukoff. The gardens collectively now have in cultivation more than 90 of the 112 recognized species in the genus, and the remaining species are gradually being obtained through requests to botanists around the world for seed.

Section 1. Evolution in Homogamic Complexes: A Review

The following section provides an overview of the conceptual framework of the experimental work on *Erythrina* and a literature review of the role of hybridization in the evolution of homogamic complexes.

Grant (1953) coined the term "hybrid complex" for groups of related species linked by occasional or frequent hybridization, and he classified different types of hybrid complex based on their reproductive mode and the means of stabilization of the hybrids. In two of these complexes the hybrid derivatives are mostly or entirely apomictic: in a clonal complex the hybrids are sterile and reproduce vegetatively, and in an agamic complex they reproduce by agamospermy. In the remaining three types of hybrid complexes, the hybrid derivatives reproduce sexually: (1) in a heterogamic complex they are permanent structural heterozygotes or permanent odd polyploids; (2) in a polyploid complex they are amphiploid with respect to the parental species; and (3) in a homogamic complex the hybrid derivatives exhibit normal meiosis and are sexual diploids, homoploid with respect to the parental species.

In some groups forming homogamic complexes, internal reproductive barriers may be present and the hybrid derivatives may be partially intersterile with the parents and with each other, as revealed by Grant's studies of annual *Gilia* (summarized in Grant, 1981). More frequently, though, particularly in complexes of perennials and woody plants, the derivatives are highly interfertile with the parents, with each other, and with all the other species in the complex: the only barriers to gametic exchange between any populations or any pair of taxa in the group are external.

Grant (1953) and Gottlieb (1972) pointed out a paradox inherent in the recombinational system of the homogamic complex that sets it apart from the other types of hybrid complex. In clonal, agamic, heterogamic, and polyploid complexes, the cytogenetic features or reproductive systems of the hybrid derivatives are important criteria of hybridity and distinguish them from the parents. In homogamic complexes the derivatives are fertile and cytogenetically homogeneous with the parents, so these criteria cannot be used as a test of hybridity. Consequently, homogamic complexes are more difficult to analyze and may pass undetected.

Grant (1953) contended that in the long term the "evolutionary potential" of homogamic complexes is much greater than in other types of hybrid complex. In the clonal, agamic, and heterogamic complexes, and to a lesser extent in polyploid complexes, favorable gene combinations are stabilized in the hybrid derivatives at the cost of a severe restriction in recombination. When environmental conditions change, the derivatives are less flexible in their capacity for genetic adaptation than are sexual diploids. Should the progenitors of the complex, the original sexual diploids, become extinct, an important source of new variation in the complex is lost.

These restrictions do not apply to homogamic complexes, however. Since the derivatives are sexual diploids, recombination is unrestricted. They are able to backcross freely with the parentals, and the original species may become extinct without jeopardizing the evolutionary potential and flexibility of the complex. Relative to the other types of hybrid complex, the homogamic complex is, in the words of Grant, an "open-ended genetic system."

The maintenance of the ability to hybridize gains importance because it extends the pool of natural variation available for recombination and selection far beyond that present in any single species. In environments undergoing climatic and/or geologic change, that "extra" genetic pool may be crucial for adaptive adjustment of the organisms, and hybrid recombinants from two or more species may have greater fitness in the newly created habitats than either of the parental species. Evolution in an open-ended homogamic complex may follow a reticulate pattern, with cycles of divergence and differentiation alternating with hybridization and recombination as environmental conditions change (Raven & Raven, 1976; Raven, 1980).

The paradox is that while hybridization is most difficult to detect and analyze in homogamic complexes, on a broad scale homogamic complexes may be much more important in plant evolution than other types of hybrid complex. Grant (1953) even speculated that hybridization in homogamic complexes may account for much of the diversity of the angiosperms, and for the reticulate nature of variation and lack of clear discontinuities between the major phyletic lines of flowering plants. Grant concluded that "the ancestral stocks may have

been hybridizing on the diploid (or diploidized) level since the earliest stages of angiosperm evolution."

Whether or not homogamic complexes have played such an important role in the evolutionary history of flowering plants, it is now well accepted that they are characteristic of the genetic structure of many large and ecologically dominant genera of trees and shrubs, at least in temperate regions. The only really thorough biosystematic study of a homogamic complex in a genus of woody plants, combining fossil evidence, experimental hybridizations, and careful field studies, is Nobs's (1963) exemplary work on *Ceanothus* in California. Many species of *Ceanothus* are dominant shrubs in the chaparral vegetation of that region, and all are diploid with $n = 12$. Nobs showed that since the Miocene, certain wide-ranging species in *Ceanothus* sect. *Cerastes* have formed hybrid swarms in areas where they have intermixed. In novel habitats created by an increasingly arid climate and by the exposure of new substrates such as serpentine outcrops, some of the hybrid derivatives have become stabilized as new self-perpetuating species.

Numerous studies have also been carried out on natural hybridization in *Quercus*, and this enormous homoploid genus ($n = 12$), which dominates the forests of much of the north-temperate zone, is generally agreed to comprise a homogamic complex (Muller, 1952; Hardin, 1975; Van Valen, 1976) or, perhaps more accurately, several homogamic complexes corresponding to its subgenera, with strong but incomplete barriers between them. The results of Cottam's long-term *Quercus* hybridization program (Cottam et al., 1982) considerably strengthen the experimental evidence (most of the previous hybridization studies in the genus merely analyzed morphological variation in natural populations).

Among other genera of trees and shrubs that probably comprise extensive homogamic complexes are *Eucalyptus* (Pryor, 1959), *Prosopis* (Simpson, 1977), and *Ribes* (Keep, 1962).

Most of the world's flora is made up of tropical woody plants, and the role of hybridization and the presence of homogamic complexes in these groups is largely unknown and remains a matter of dispute. Many systematists who work on tropical woody genera evidently believe that hybridization is absent or unimportant in the organisms they study, e.g., Ashton's (1969) comments on Dipterocarpaceae in Southeast Asia. Ehrendorfer (1970) thought that narrower "niche width" restricted gene flow, and a higher incidence of polyploidy and apomixis in tropical tree species made them much less likely to hybridize than their temperate-zone counterparts. It does appear logical that in species-rich tropical forests population density is low and neighborhood size is small for any one species, as well as for groups of sympatric congeners, so the opportunities for hybridization may be fewer and the hybrids harder to detect than, for example, in a temperate forest with large populations of sympatric *Quercus* species.

At any rate, the critical experimental hybridization trials have not been carried out for tropical woody plants, except for a few economically important genera. For example, strong sterility barriers have been found between Amazonian species of *Theobroma* (Addison & Tavares, 1952). In contrast, *Hevea* in the same region is probably a homogamic complex. In this homoploid genus ($n = 18$), fertile hybrids were easily obtained in experimental gardens, and numerous natural hybrids were reported (Seibert, 1947).

In many genera of tropical woody plants, all or most species share the same relatively high chromosome number and may be considered diploidized paleopolyploids. Thus, most genera of Bignoniaceae have the same chromosome number of $n = 20$; they are probably paleohexaploids based on $x = 7$ (Goldblatt & Gentry, 1979). Such plant groups may be prime candidates for the formation of homogamic complexes. Until the present study, however, a thorough biosystematic investigation on the scale of Nobs's work on *Ceanothus* had not been carried out on any large tropical woody genus or, in fact, on any other woody genus.

Section 2. History and Relationships of the Genus

Erythrina L. comprises about 112 species distributed throughout the tropical regions of the world and extending into warm-temperate areas such as South Africa, the Himalayas and southern China, the Rio de La Plata region of Argentina, and the southern United States (Krukoff & Barneby, 1974) (Fig. 1). Most species are trees or shrubs, but about 10 species occurring in climates with pronounced dry and/or cool seasons are perennial herbs with large woody rootstocks. *Erythrina* species occur in a very wide variety of habitats, from lowland tropical rainforest to very arid subtropical deserts to highland coniferous forests above 3,000 m.

The distinctiveness of *Erythrina* has long been recognized by legume systematists. Following Bentham (1865), the genus has been placed traditionally in the subtribe Erythrininae of the tribe Phaseoleae, a relationship based principally on the characteristic trifoliolate leaves that *Erythrina*

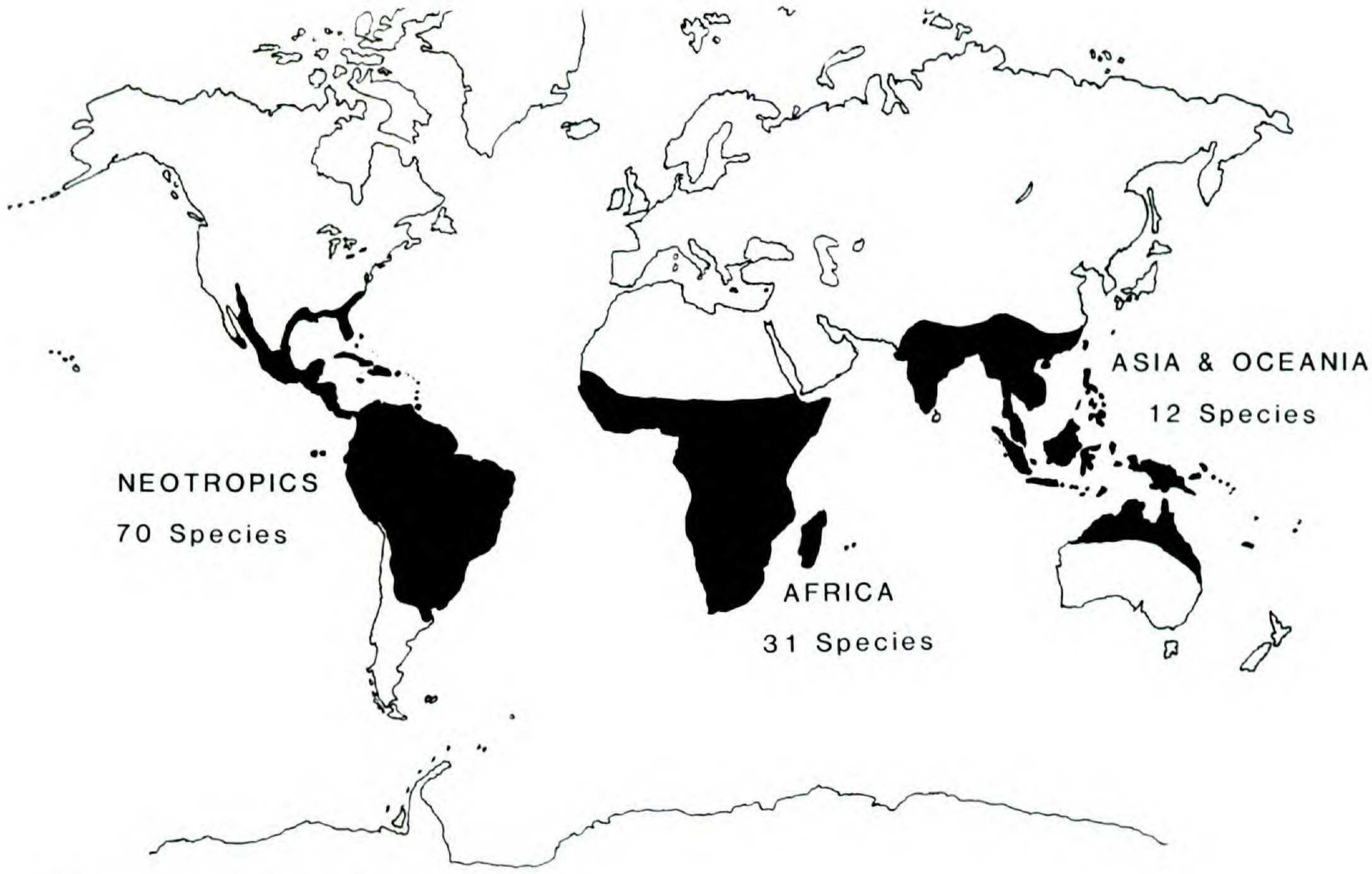


FIGURE 1. *Distribution of* Erythrina.

shares with the rest of the Phaseoleae. In a recent generic treatment of Phaseoleae, Lackey (1981) maintained the traditional classification but remarked that "the relationship of [*Erythrina*] to the remainder of the Papilionoideae is an absolute mystery . . . the genus would have long ago been accommodated outside the Phaseoleae had not the foliage suggested this tribe. In many significant characters, *Erythrina* stands alone among the Phaseoleae."

Besides *Erythrina*, the subtribe Erythrininae contains the genera *Mucuna*, *Strongylodon*, *Butea*, *Apios*, *Spatholobus*, *Cochlianthus*, *Rhodopsis*, and *Neorudolphia*. The relationships among these genera are not close and the erection of the subtribe is largely a matter of convenience to accommodate a loose assortment of genera not easily placed in other subtribes of the Phaseoleae.

Butea alone, the only other arborescent genus in the Phaseoleae, appears to have some true affinities with *Erythrina*. Baretta-Kuipers (1982) found that the unusual wood anatomy of *Erythrina* is very similar to that of *Butea*. In many other important traits, however, *Erythrina* is distinct from *Butea* and from all other legumes. The base chromosome number of $x = 21$, shared by all 86 *Erythrina* species that have been counted, is unique in the Leguminosae and indicates no direct relationship with *Butea* with $n = 9$. The unusual, high activity–low affinity nitrate reductase system present in all *Erythrina* species that have been examined differs in some respects from known nitrate reduction patterns in other angiosperms (Orebamjo et al., 1982). Neither *Mucuna* nor *Butea* (G. R. Stewart, pers. comm. to P. Raven, 1984) shares this trait with *Erythrina*. The *Erythrina* alkaloids, structurally complex isoquinolines nearly universal in the seeds of the genus, are found in no other legumes (Mears & Mabry, 1971).

Although *Erythrina* is quite distinct from the rest of the Leguminosae, and despite its great ecological and morphological diversity, the cytological and phytochemical evidence cited above and the interfertility relationships presented in this paper indicate that the genus is unusually close-knit for its size (Raven, 1974), and there is no doubt that it is monophyletic. As such, the genus is an ideal subject for the biosystematic study of diversification of an entire evolutionary clade.

The origin of *Erythrina*, like its relationship to the rest of the Leguminosae, is obscure. No fossil record of the genus has been reported. In the light of its distribution patterns, pollination, and dispersal mechanisms, and the known history of Leguminosae as a whole, Raven (1974) postulated an Upper Eocene to Upper Oligocene origin for the genus (40–30 m.y. BP), followed by ocean-drift and/or other long-distance dispersal among the

three principal tropical regions of America, Africa, and Asia–Oceania. Much diversification of *Erythrina* has occurred independently in Africa and America and to a lesser extent in Asia.

The place of origin of *Erythrina* is unknown, but South America appears most likely since the majority of the putative ancestral groups (as considered by Krukoff & Barneby, 1974) within the genus are found there. Africa is also a possible candidate, since it likewise contains a number of endemic groups. Although *Erythrina* almost certainly originated well after the breakup of West Gondwanaland, it has a basically South American–African distribution that is shared by many angiospermous groups, including the Leguminosae itself (Raven & Axelrod, 1974). The *Erythrina* taxa in "tropical Laurasia," i.e., Asia and Mesoamerica, are clearly derived groups. In Mesoamerica the genus has undergone extensive recent speciation within a single lineage.

PATTERNS OF DIVERSIFICATION: POLLINATION

Erythrina species exhibit a great diversity in floral structure, inflorescence orientation, fruit morphology, seed coat coloration, and vestiture and epidermal ornamentation of foliage and calyces. The infrageneric classification of *Erythrina* is based principally on these characters.

The diversity of floral structure reflects adaptive radiation in *Erythrina* with respect to pollination mechanisms. All *Erythrina* species have red or orange flowers and copious nectar, and are adapted to pollination by nectarivorous birds. There are two distinct syndromes of ornithophily in the genus. All 42 Old World species and 15 of the 70 New World species are pollinated by "perching birds" of several families in the order Passeriformes. Passerine birds cannot hover efficiently or for any length of time, and the inflorescences of passerine-pollinated *Erythrina* are oriented in such a way that the birds can perch while feeding on floral nectar. The corolla standard is usually broad, and the flowers are open, with exposed reproductive parts. Pollen is deposited on the feeding bird's breast. The flowers of passerine-pollinated species of *Erythrina* are diverse in size, form, and orientation, which appears to reflect the variation in size, morphology, and behavior of the pollinators, which range from sunbirds and white-eyes weighing 8–10 g to orioles weighing over 35 g.

The remaining 55 New World species of *Erythrina* (nearly half the genus) are pollinated by hummingbirds (Trochilidae). Hummingbirds are the most specialized of nectarivorous birds and the only ones that hover while feeding. The corolla standard of hummingbird-pollinated *Erythrina* is narrow and conduplicately folded to form a "pseudotube," concealing the wing and keel petals as well as the reproductive parts. The flower resembles the tubular corollas of many gamopetalous hummingbird-pollinated plants, but in *Erythrina* the pseudotube is not sealed on the ventral side where the margins of the corolla standard meet. The inflorescence axis of the hummingbird-pollinated species is erect, and the flowers are oriented outward, providing no perch for the hovering hummingbirds.

Only a small number of the 315 neotropical hummingbird species are *Erythrina* pollinators, and these are all similar in size, bill length, and behavior. The *Erythrina* pollinators are principally specialized "high-reward trapliners," nonterritorial species that follow regular daily foraging routes between widely separated individual plants (Neill, 1987). The flowers of the hummingbird-pollinated *Erythrina* species are much more uniform in size and shape than those of the passerine-pollinated species, and this probably reflects the relative uniformity of pollination mechanisms among the former group.

FRUITS, SEEDS, AND DISPERSAL

The diverse fruit and seed characteristics of *Erythrina* species are indicative of adaptation for different dispersal mechanisms. The putative ancestral species (Krukoff & Barneby, 1974) inhabit coastal, estuarine, or riverine environments and have dull brown floating seeds transported by oceanic or fluvial currents. These species are effective colonizers: *Erythrina fusca* and *E. variegata* both became established on the island of Krakatoa a few years after the cataclysmic eruption of 1883 (Guppy, 1906). Since the review of Raven (1974), new anecdotal evidence has come to light concerning the dispersal of these seeds and their viability following long exposure to salt water. A drift seed of *Erythrina variegata* was recorded after a storm on the beach of Canton Island, a low coral atoll at 3°S latitude in the western Pacific, where *Erythrina* does not occur. The nearest possible source for the drift seed is Samoa, 700 km to the south. The seed, planted in Hawaii, grew into a 20-m tree (from herbarium label of *Degener 35066*, BISH).

Alone in *Erythrina*, *E. subumbrans* of Asia–Oceania has winged, wind-dispersed fruits. The Tanzanian endemic *E. greenwayi* has unusual fruits with narrow winglike ridges, but the fruits are heavy and do not appear to be effectively wind dispersed.

Most of the putative derived species of *Ery-*

thrina have bright red seeds, which persist in conspicuous display on the pods after dehiscence. Red seeds have evidently evolved independently in several lineages of *Erythrina*; one or two species in each lineage have bicolored red and black seeds. The red or red-and-black seeds are presumed to be "imitation arils" (Ridley, 1930) or mimetic berries. According to this theory, they are eaten by frugivorous birds attracted by the bright colors and are dispersed when they pass through the digestive tract unharmed, but there are few actual reports of such "mistake" dispersals. Skutch (1971) recorded an overwintering yellow-throated vireo (*Vireo flavifrons*) eating red *Erythrina* seeds in Costa Rica. I have seen this phenomenon on only one occasion, when in March 1983 in Chiapas, Mexico, I observed a migrant wood thrush (*Hylocichla mustellina*) ingest several red seeds of *Erythrina folkersii* displayed on the pods. A major autumn food item of this bird in eastern North America, before it migrates south, is the bright red, fleshy fruit of *Cornus florida*, which *Erythrina* seeds resemble quite closely (E. Morton, pers. comm.). Thus the dispersal of *Erythrina* seeds as mimetic berries by "naive" migrant birds does seem to be a real, though perhaps infrequent, phenomenon.

The "mimetic berry" theory is fraught with all of the conceptual difficulties common to considerations of the evolution of mimicry. The alkaloids in the seeds of *Erythrina* are toxic, and the deceived bird must survive the passage of the seed through its gut if it is to produce subsequent generations of birds that will disperse subsequent generations of *Erythrina*. (The alkaloids are not released unless the seed coat is broken, and frugivorous birds do not have strong gizzards to grind seeds.) Additionally, the mimic should be rare relative to the model, and the deception must occur frequently enough so that natural selection can act upon it. The question of mimetic seed coloration in *Erythrina* and other legumes is discussed in McKey (1975).

FEATURES OF THE EPIDERMIS

A great variety of special epidermal structures occurs in *Erythrina*, particularly on the abaxial leaf surfaces. These include hairs of many types, epidermal papillae and various "lamellae," and epicuticular wax deposits. The adaptive significance of these features is not known, but they are often diagnostic for particular species or species groups and often aid in identification of sterile material. Patterns of leaf epidermal features and their inheritance in interspecific hybrids are discussed later.

SUBDIVISIONS OF *ERYTHRINA*

The first formal subdivision of *Erythrina* was established by Harvey (1861), with subsequent treatments by Harms (1915), Louis (1935), and Krukoff (1939a, for the American species; 1939b, for the Asiatic–Polynesian species). In the 19th century a number of generic segregates were proposed based on the distinctive floral morphs of certain groups of species: e.g., *Chirocalyx* Meisn., *Micropteryx* Walp., *Duchassaingia* Walp., and *Hypaphorus* Hassk. These segregates were treated as sections or subgenera of *Erythrina* by later monographers. The modern classification of the genus was established by Krukoff & Barneby (1974), who recognized 5 subgenera and 26 sections. I accept their treatment as the systematic basis for the present work; a few taxonomic changes to be published later are anticipated in this paper prior to their formal designation. The infrageneric classification of *Erythrina* is summarized in Table 1. A list of the currently recognized species, with authorities and with changes in synonymy made since Krukoff & Barneby's (1974) conspectus of the genus, is included in Appendix I.

The sections of *Erythrina* are well delimited morphologically and biogeographically, and each appears to be monophyletic. The subgenera also are delimited by several good characters and appear monophyletic, except for the large and heterogeneous subg. *Erythrina*, which includes 70% of the species in the genus. The relationships of the sections comprising subg. *Erythrina* to one another still present a number of unresolved taxonomic and phylogenetic questions.

The following is a short narrative synopsis of the infrageneric classification of *Erythrina* and an outline of evolutionary and biogeographical trends; in the discussion, the taxa used in the experimental studies are emphasized.

Subgenus *Micropteryx* is restricted to South America, except for *Erythrina fusca* in the monotypic sect. *Duchassaingia*. With floating seeds dispersed by ocean currents, *E. fusca* is the only species in the genus to occur in both the Old World and the New World. It is widely distributed along coasts and rivers in the Neotropics and Asia–Oceania, as well as in Madagascar and the Mascarene Islands, but its present native range does not include continental Africa. It often occurs in extensive pure stands in seasonal swamps. With its

TABLE 1. *Infrageneric classification of* Erythrina.

Sections		Number of Species	Distribution		
			America	Africa	Asia–Oceania
I.	Subg. *Micropteryx*				
1.	*Duchassaingia*	1	X	X (Madagascar)	X
2.	*Cristae-galli*	2	X		
3.	*Micropteryx*	4	X		
II.	Subg. *Erythrina*				
4.	*Suberosae*	4			X
5.	*Arborescentes*	1			X
6.	*Hypaphorus*	1			X
7.	*Breviflorae*	4	X		
8.	*Edules*	2	X		
9.	*Stenotropis*	1	X		
10.	*Pseudo-edules*	2	X		
11.	*Leptorhizae*	4	X		
12.	*Erythrina*	36	X		
13.	*Gibbosae*	1	X		
14.	*Corallodendra*	9	X		
14a.	*Fidelenses*	1	X		
15.	*Cubenses*	1	X		
16.	*Olivianae*	1	X		
17.	*Caffrae*	2		X	
18.	*Humeanae*	2		X	
19.	*Acanthocarpae*	1		X	
III.	Subg. *Tripterolobus*				
20.	*Tripterolobus*	1		X	
IV.	Subg. *Chirocalyx*				
21.	*Bruceanae*	1		X	
22.	*Macrocymbium*	2		X	
23.	*Dilobochilus*	1		X	
24.	*Dichilocraspedon*	1		X	
25.	*Chirocalyx*	14		X	
V.	Subg. *Erythraster*				
26.	*Erythraster*	13	X	X	X

wide distribution and presumably primitive features (Krukoff & Barneby, 1974), *E. fusca* or a *fusca*-like ancestor may represent the original progenitor of the entire genus.

Section *Cristae-galli* includes two species, *E. crista-galli*, which forms extensive populations along the estuary of the Río de La Plata in extratropical South America, and *E. falcata*, which inhabits the "Yungas" forest of the eastern Andean foothills and similar subtropical forest vegetation in southeast Brazil. The four species of sect. *Micropteryx* inhabit riverine or upland forests of the Amazon and Orinoco basins and the Planalto of Brazil.

Subgenus *Erythrina*, with 79 species in 17 sections, is distributed throughout the three major tropical regions of America, Africa, and Asia, but no single section occurs in more than one of these areas. The subgenus includes all 55 of the American hummingbird-pollinated species in six different sections which I believe to have been derived from passerine-pollinated groups by convergent evolution in several independent lineages.

Erythrina speciosa of coastal Brazil, in the monotypic sect. *Stenotropis*, is geographically and phylogenetically isolated from the rest of the hummingbird-pollinated species. The herbaceous, hummingbird-pollinated species of sect. *Leptorhizae*, endemic to central Mexico, are probably derived directly from the passerine-pollinated shrubby/ar-

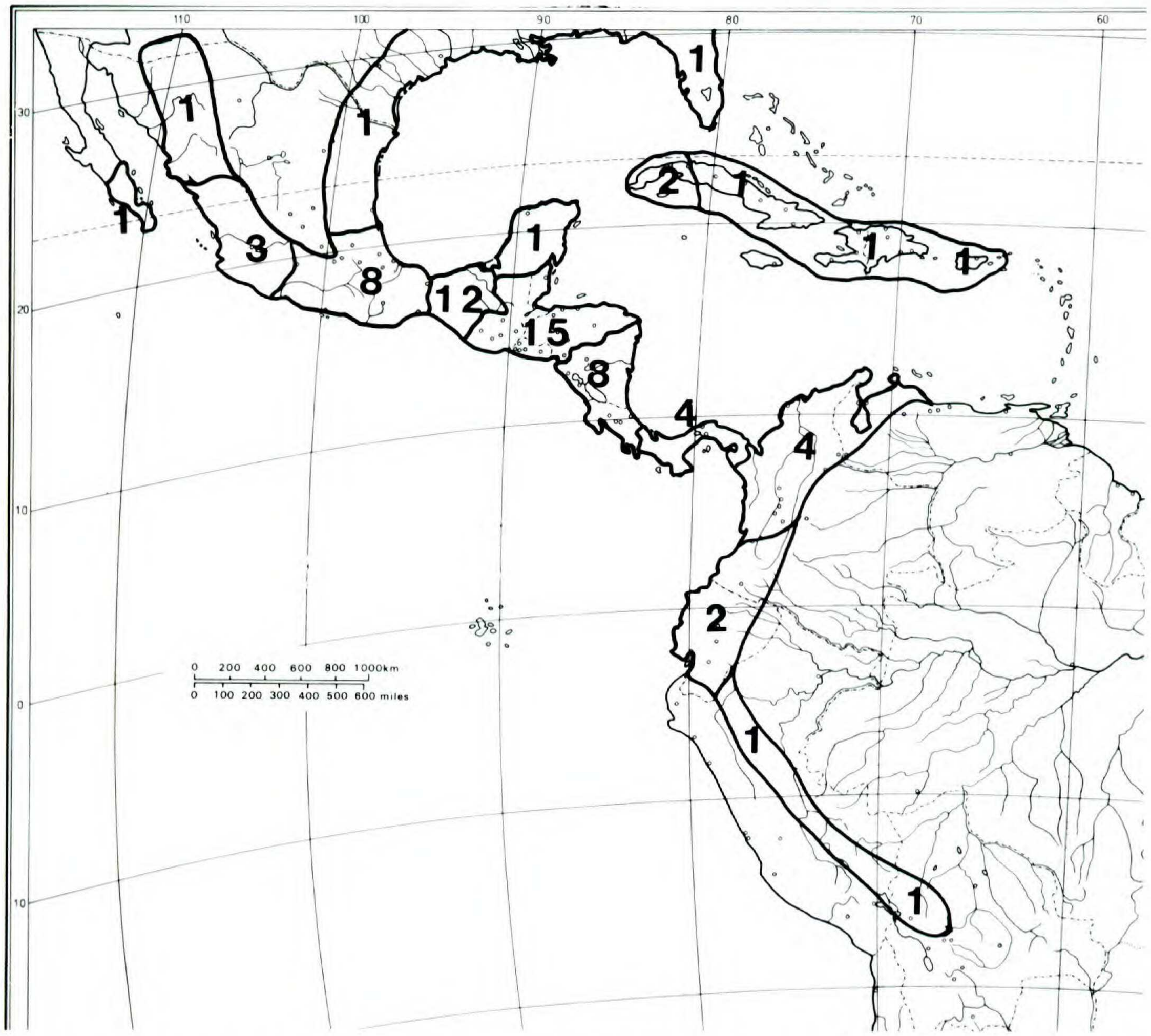


FIGURE 2. *Distribution of* Erythrina *sect.* Erythrina. *The numbers indicate the numbers of species known to occur in each geopolitical region bounded by the heavy black lines.*

borescent sect. *Breviflorae* endemic to the same region. In a parallel manner, the Andean hummingbird-pollinated sect. *Pseudo-edules* may be derived from the Andean passerine-pollinated sect. *Edules*.

The large Mesoamerican-centered, hummingbird-pollinated sect. *Erythrina* (36 species) is closely allied with the remaining hummingbird-pollinated sections; *Corallodendra*, with 9 species in South America and the Antilles, and the monotypic sections *Gibbosae* in southern Central America, and *Cubenses* endemic to Cuba. The relationship of these advanced arborescent hummingbird-pollinated groups to the rest of the genus is not clear, however.

Figure 2 shows the distribution of sect. *Erythrina* and the number of species known to occur in geomorphologically and politically delimited subregions of its range. The greatest concentration of species is in nuclear Central America, particularly in the Mexican state of Chiapas and in Guatemala. Geologically, nuclear Central America is much older than southern Central America. It has been connected to the North American continent since the Cretaceous, whereas southern Central America was only a chain of volcanic islands until the close of the Panamanian isthmus in the Pliocene (Raven & Axelrod, 1974; Coney, 1982). It is most probable that sect. *Erythrina* originated in nuclear Central America following migration of its progenitor from South America, an event that could have occurred either before or shortly after the final formation of the southern Central American land bridge. Species of this section, which comprises nearly one-third of the entire genus, inhabit nearly every forested habitat in the geologically active and climatically complex Mesoamerican region. In contrast to *Erythrina fusca* and other species that

form extensive monospecific stands, the species of sect. *Erythrina* generally occur at low population densities. Many have a restricted geographic range and occur in a single vegetation type, in a rather narrow altitudinal belt, or only on particular substrates, such as outcrops of calcareous rock. Sympatry among species in the section is rare, but when it does occur, natural hybrids are generally found. All available evidence indicates that sect. *Erythrina* is an outstanding example of rapid adaptive radiation and speciation in the recent geological past.

The remaining sections of subg. *Erythrina* occur in the Old World, and their affinities to the American sections are not apparent. The South African endemic sects. *Caffrae*, *Humeanae*, and *Acanthocarpae* are the only representatives of the subgenus on that continent. Certain floral, fruit, and seed features of sect. *Caffrae* do suggest an affinity with the monotypic Mexican sect. *Oliviinae*, but a plausible explanation of such a connection is difficult to imagine.

The Asian sects. *Suberosae*, *Arborescentes*, and *Hypaphorus* are an autochthonous group with mostly "primitive" features and do not appear to be closely allied with the American and African sections of subg. *Erythrina*. The species of sect. *Suberosae* possess one singularly "advanced" feature: complex reticulate "lamellae" formed by epidermal cells of the abaxial leaf surfaces (this paper, Section 5).

The monotypic subg. *Tripterolobus*, consisting of *E. greenwayi* and endemic to a small area in the Rift Valley of Tanzania, is an evolutionary anomaly. The three-winged follicular pod is unique in the genus, while the flower, as Krukoff & Barneby (1974) indicated, seems constructed from disparate elements of different subgenera.

Subgenus *Chirocalyx*, with 5 sections and 19 species, is restricted to sub-Saharan Africa. Section *Chirocalyx* comprises 14 species which inhabit environments as diverse as the Kalahari Desert, the lowland rainforests of Cameroon, the vast savannas of the Sahel, and the montane forests of eastern Zaire—a radiation reminiscent of sect. *Erythrina* in Mesoamerica, although with fewer species. The remaining sections in subg. *Chirocalyx* are mono- or ditypic, each quite distinct morphologically.

The final subgenus is *Erythraster*, with 13 species in the sole sect. *Erythraster*. It is basically an Old World group with two disjunct, derived species in the Neotropics. *Erythrina variegata*, the coastal-strand, ocean-dispersed species, occurs from Tanzania and Madagascar around the shores of the Indian Ocean and westward through Indonesia, New Guinea, Polynesia, and Micronesia to the Marquesas. The remaining species inhabit upland areas, including four in East Africa and one in Australia. There is one endemic species on each of the islands or island groups of Madagascar, Java-Bali, New Guinea, Tahiti, and the Hawaiian archipelago, and each of these may be derived independently from *E. variegata*. The disjunct *E. velutina*, widely distributed in dry forests of northern South America, the Galapagos, and the Antilles, and its Cuban endemic derivative, *E. grisebachii*, form a distinct species complex together with the Tahitian *E. tahitensis* and the Hawaiian *E. sandwicensis*. All the species of this Polynesian–Neotropical complex have "mimetic berry" red seeds, unlike *E. variegata* and most of the other species in sect. *Erythraster*. *Erythrina variegata* is present on Tahiti but not in Hawaii or the Neotropics. With this pattern of distribution, it appears most likely that these Polynesian–Neotropical disjuncts were established following long-distance dispersal by birds across the Pacific, and not by ocean-drift of *E. variegata* or a *variegata*-like ancestor.

Section 3. Chromosome Numbers and Meiotic Behavior in Diploid and Polyploid Species

Erythrina is well known to be relatively uniform cytologically; polyploidy is rare, and aneuploidy is unknown (Lewis, 1974; Goldblatt, 1981a, 1984). The basic chromosome number of the genus is $x = 21$, unique in Leguminosae. Of the 65 species counted prior to the present study, 61 are diploid ($2n = 42$), two are tetraploid ($2n = 84$), one has reports of both diploid and tetraploid races, and one has reports of hexaploid ($2n = 126$) and octoploid ($2n = 168$) races.

The base number for Phaseoleae and probably for subtribe Erythrinineae is $x = 11$, and reduction to $n = 10$ is common in the tribe. *Erythrina* is likely either an allotetraploid based on $n = 11 + n = 10$ or a hypotetraploid $n = (11 \times 2) - 1$ (Goldblatt, 1981b), and thus a paleopolyploid genus.

MATERIALS AND METHODS

Floral buds were collected from trees in cultivation at three botanical gardens in Hawaii: Pacific Tropical Botanical Gardens in Lawai (PT); Waimea Arboretum in Haleiwa (WA); and Ho'omaluhia Botanic Garden in Kaneohe (HO). Floral buds and/or seeds were collected from wild populations of certain species in Mexico and Costa Rica.

For gametic counts and meiotic analyses, floral buds in developmental series were fixed either in 3:1 ethanol:acetic acid or in 6:3:1 chloroform:ethanol:acetic acid, which generally provided better fixation. After 1–2 weeks in the fixative at room temperature, buds were transferred to 70% ethanol and stored below 5°C. Anthers were squashed in acetocarmine with Hoyer's solution added (Beeks, 1955) to make permanent slides.

For somatic counts, seeds obtained from wild populations were germinated on filter paper. The primary root tips were pretreated in 0.003 M 8-hydroxyquinoline for 4 hours at room temperature, fixed in 3:1 ethanol:acetic acid for 2–12 hours, and hydrolyzed in 10% HCl for 10 minutes at 60°C. Root tips were squashed in FLP orcein (Jackson, 1973).

Slides were examined under phase contrast with a Zeiss Universal microscope; chromosomal configurations were photographed with Zeiss MC63 equipment using Kodak Technical Pan film developed for high contrast.

RESULTS

Chromosome Numbers. Chromosome counts and voucher data are listed in Table 2. For cultivated material the original wild-collected voucher is cited if it exists; if not, a voucher made from the garden progeny is cited. All vouchers are deposited at Missouri Botanical Garden (MO) unless otherwise noted.

The gametic count of $n = 42$ for *E. amazonica* reconfirms earlier somatic counts of $2n = 84$ (Atchison, 1947; Goldblatt & Davidse, 1977) for this tetraploid. This species is distributed throughout the northern Amazon basin and in the Guianas, but all the chromosome counts to date have been obtained from populations in the Brazilian state of Maranhão. A more complete sampling of the species range may reveal infraspecific variation in ploidy level, as has been determined for other species with polyploid strains.

My count of $n = 21$ for the tropical Asian *Erythrina suberosa* is diploid and agrees with 13 previous reports for the species. Mehra (1976), however, reported $n = 42$ in three populations in the western Himalayas, at its geographic margin and altitudinal upper limit. As with *E. amazonica*, a cytogeographic survey of ploidy level in *E. suberosa* is desirable.

With the exception of *Erythrina macrophylla*, the remaining 22 chromosome counts listed in Table 2 are all first reports for species. All are diploid ($n = 21$ or $2n = 42$) except the octoploid *E. burana* ($n = 84$). This Ethiopian endemic is closely related to *E. burttii*, which ranges from Ethiopia south to Tanzania, and for which both hexaploid ($2n$ = ca. 126; Atchison, 1947) and octoploid ($2n$ = ca. 168; Goldblatt, 1981a) counts have been obtained.

Chromosome numbers are now known for 86 of the 112 species of *Erythrina* recognized here. Eighty-one species (94%) are diploid, with the remaining 5 species (6%) polyploid or variable in ploidy level. The polyploid species are all in different sections and are not closely related to one another, with the exception of *E. burttii* and *E. burana*. Polyploidization has thus occurred at least four times independently in *Erythrina*. Given the rarity of polyploidy in the genus, it seems likely that the closely related *E. burttii* and *E. burana* were derived from a common polyploid ancestor.

Chromosome counts have yet to be obtained from 25 species of *Erythrina*. Eleven of these are from Africa where three of the five known polyploids occur. Seven uncounted species are South American, where *E. amazonica* is the only polyploid known. Polyploidy is unknown for *Erythrina* in North and Central America, where 42 of the 45 native species have been counted.

Meiosis in Diploid Species. Chromosome size, morphology, and meiotic behavior were similar in all species examined. Observations of individuals of two typical diploid species, *Erythrina berenices* (WA 81s505) and *E. macrophylla* (PT 750420001), are described and illustrated here.

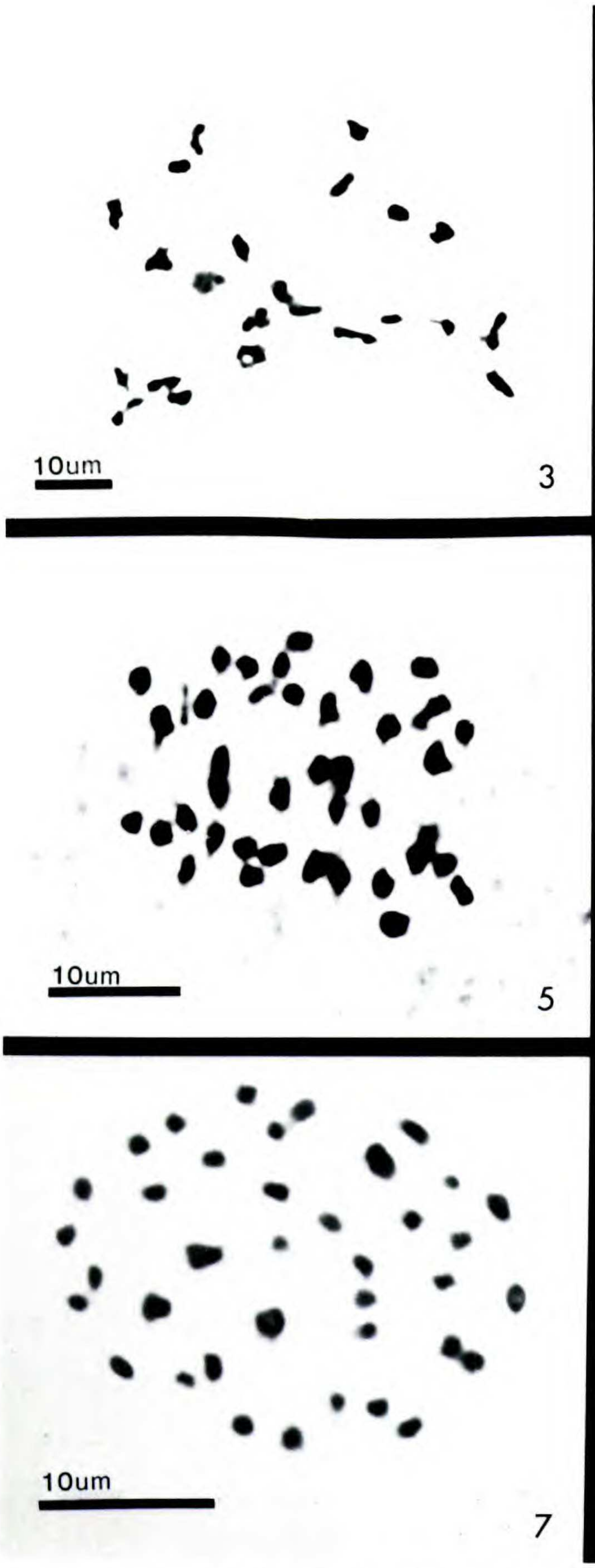
Observations of chromosome pairing at zygotene and pachytene are desirable in meiotic analyses (Jackson, 1984), but these were not feasible in *Erythrina* because of its high chromosome numbers. At diakinesis, 21 bivalents were regularly formed. Each bivalent had either one or two terminal chiasmata. In *E. macrophylla*, the average number of chiasmata per cell was 31.5 ± 1.84 out of 10 cells sampled. This accords with the figures of 31.35 ± 0.54, 31.25 ± 0.61, and 32.08 ± 0.7 chiasmata per cell reported by Jalil et al. (1982) for, respectively, *E. variegata*, *E. resupinata*, and their F_1 hybrid *E.* ×*resuparcellii*.

At early to mid diakinesis, the bivalents were generally well separated, thus the gametic chromosome counts listed in Table 2 were usually made at this stage. Toward the later stages of diakinesis and as the nucleolus began to disintegrate, groups of two or more bivalents appeared clumped together in the cell (Fig. 3). Thin strands of chromatin were frequently observed to stretch between bivalents.

TABLE 2. *Chromosome counts of* Erythrina *species reported in this paper. Vouchers are housed at MO unless otherwise indicated.*

Species	$n =$	$2n =$	Voucher Data
E. amazonica Krukoff	42		WA 76s449, cultivated. Brazil. Maranhão: Lapela, *N. T. Silva 4238* (NY).
E. batolobium Krukoff & Barneby	21		Missouri Botanical Garden, cultivated (from wild-collected rootstock). Mexico. Guerrero: Filo de Caballo, 6,300 ft., oak forest, *Neill 5647*.
E. berenices Krukoff & Barneby	21		WA 81s505, cultivated. Mexico. Veracruz: Tlalnelhuayocan, *H. Perales s.n.* in 1981 (NY).
E. breviflora A. DC.	21		Mexico. Guerrero: *H. Iltis 28655*.
E. burana R. Chiovenda	84		PT 740435001, cultivated. Ethiopia. Locality unknown: *F. Meyer s.n.* in 1974. Voucher from cult.: *Neill 5716*.
E. cochleata Standley	21		Costa Rica. Heredia: La Virgen, 10 km SW of Puerto Viejo, 200 m, *Neill 5102*.
E. elenae Howard & Briggs	21		WA 80s614, cultivated. Cuba. Cienfuegos: *Centro de Investigación Forestal s.n.* Voucher from cult.: *Neill 5078*.
E. florenciae Krukoff & Barneby		42	Mexico. Chiapas: Motozintla, Cerro Mozotal, 6,600 ft., *Neill 5600*.
E. gibbosa Cuf.	21		Costa Rica. Alajuela: Cordillera de Tilarán, upper Peñas Blancas valley, below Monteverde reserve, 1,300 m, *Neill 5028*.
E. globocalyx Porsch & Cuf.	21		Costa Rica. San José: Las Nubes, 1,700 m, *Neill 5033*.
E. hondurensis Standley	21		HO 80.037, cultivated. Honduras. Tela: *Hazlett s.n.* in 1980. Voucher from cult.: *Neill 5709*.
E. horrida A. DC.		42	Mexico. Oaxaca: 2 km E of Ixtlán, road to Yavesia, 2,030 m, *M. Sousa 12634* (MEXU).
E. leptorhiza A. DC.	21		Mexico. México: Municipio Ixtapaluca, old Hwy. 190, km 25, 8,300 ft., *Neill 5646*.
E. macrophylla A. DC.	21		PT 750420001, cultivated. Guatemala. Sololá: Godinez, 6,145 ft., *B. A. Krukoff 1975-4* (NY).
E. mexicana Krukoff		42	Mexico. Oaxaca: 14 mi. SW of San Jeronimo Miahuatlán, 4,800 ft., *Neill 5423*.
E. oaxacana (Krukoff) Krukoff		42	Mexico. Oaxaca: 9 km N of Diaz Ordaz, road to Cuajimolaya, 7,700 ft., *Neill 5409*.
E. pudica Krukoff & Barneby	21		Mexico. Chiapas: 15 mi. E of Cintalapa, Hwy. 190, 2,000 ft., *Neill 5440*.
E. sacleuxii Hua	21		WA 74p1296, cultivated. Kenya: Arabuko forest, near coast, *Lavranos 11225* (NY).
E. sigmoidea Hua	21		PT 740192001, cultivated. India: locality unknown, cultivated, *D. A. Millington s.n.* in 1974. Voucher from cult.: *Neill 5715*.
E. smithiana Krukoff	21		PT 740329001, cultivated. Ecuador. Guayas: Manglaralto. *MacBryde & Herrera-MacBryde 690* (NY).
E. sousae Krukoff		42	Mexico. Oaxaca: 14 km S of San Miguel Suchixtepec, 2,100 m, *Neill 5425*.
E. suberosa Roxb.	21		WA 75s960, cultivated. India: Matrimandir Gardens, cultivated. Voucher from cult.: *Neill 5273*.
E. tahitensis Nad.	21		PT 770442001, cultivated. Tahiti: Manupa Ridge, 2,000 ft., *Perlman s.n.* in 1977. Voucher from cult.: *Neill 5177*.
E. tuxtlana Krukoff & Barneby	21		Mexico. Chiapas: 26 km N of Ocozocuautla on road to Malpaso, 2,100 ft., *Neill 5486*.

The characteristic clumping of two or three bivalents became even more common in metaphase I. At anaphase I, long strands of chromatin were frequently observed stretching between disjoining chromosomes, even after the main bodies of the chromosomes were separated by a considerable distance on either side of the equatorial plate (Fig. 4).



FIGURES 3–8. *3–6. Meiosis in pollen mother cells, diploid species of* Erythrina.—*3. Late diakinesis,* E. berenices, *WA 81s505* (n = *21*). *Clumping of bivalents.*—*4. Anaphase,* E. berenices, *WA 81s505. Sticky chromatin bridges stretch between disjoined chromosomes.*—*5, 6. Anaphase,* E. macrophylla, *PT 750420002* (n = *21*). *Late disjunction of some bivalents.*—*7. Mitosis in root tip cell of diploid* E. horrida, Sousa 12634 (2n = *42*). *Somatic chromosomes are not clumped.*—*8. Diakinesis in pollen mother cell of tetraploid* E. amazonica, *WA 76s449* (n = *42*). *Two quadrivalents are circled.*

The chromatin connections between disjoining chromosomes appeared to be in all cases simply "matrix bridges" caused by chromosome "stickiness" (Beadle, 1932). Based on observations at subsequent stages, it is unlikely that any of the observed "bridges" were true dicentric bridges or any other configuration resulting from chromosomal inversions or translocations.

Another frequently observed phenomenon was late disjunction of one or several bivalents at anaphase I (Figs. 5, 6). One or two lagging bivalents were often present even at late anaphase I when most chromosome pairs were completely separated. However, observations of cells at later stages revealed no evidence of nondisjunction or unequal assortment of chromosomes.

In contrast to the chromosome "stickiness" and secondary association of bivalents at meiosis, somatic pairing of homologues was not observed in mitotic root-tip cells. A typical mitotic configuration of the diploid species *Erythrina horrida* ($2n = 42$) is shown in Figure 7, where there is no evidence of pairing or of sticky chromatin connections between chromosomes.

Meiosis in pollen mother cells of the Asian *E. variegata* (as *E. indica* Lam.) was depicted by Sundar Rao (1945) and in several additional Asian species by Mehra (1976). Both reported postsynaptic secondary association of chromosomes at metaphase I and subsequent stages to be common in some species. Mehra (1976) reported aberrant meiosis with 13–21 bivalents, 0–16 univalents, and 0–2 B chromosomes in a diploid strain of *E. suberosa*, while a tetraploid strain of the same species exhibited normal meiosis with 42_{II}. Jalil et al. (1982) reported normal meiosis with 21_{II} in the artificial hybrid *E.* ×*resuparcellii* (*E. resupinata* × *E. variegata*).

Pollen fertility, as estimated by Alexander's double stain technique (Alexander, 1969) was uniformly high in all *Erythrina* species examined. Seventeen individuals belonging to eight species, used as parentals in the experimental hybridization trials, had a mean pollen fertility of 95% (at least 500 grains counted per sample). Such high fertility suggests that the chromatin "bridges" and late disjunction of bivalents observed in most cells at anaphase I are not indicative of meiotic aberrations, do not result in a high frequency of aborted cells, and therefore most cells receive the correct complement of 21 chromosomes following meiosis I and II.

Meiosis in Polyploid Species. Among the tetraploid species of *Erythrina*, only a single strain of *E. amazonica* was available for analysis (WA 76s449; PT 760356001). In several individuals of this strain, 42 bivalents were observed in some cells at diakinesis and metaphase I, while in others one or two quadrivalents were clearly visible (Fig. 8). In contrast to the merely "sticky" postsynaptic associations seen in the diploids, the quadrivalents in *E. amazonica* appeared to be true multivalents resulting from synaptic pairing at prophase. The configuration of this species at meiosis I, then, is $38–42_{II}$ and $2–0_{IV}$. The formation of occasional quadrivalents did not disrupt normal disjunction, however, as no cells at telophase I or subsequent stages were observed with other than 42 chromosomes.

At diakinesis and metaphase I of the octoploid *E. burana*, considerable clumping of chromosomes was evident in all cells examined. With a large number of chromosomes crowded together, the configurations were not completely resolvable and it was not possible to determine whether synaptic multivalents were actually formed.

DISCUSSION

The postsynaptic secondary association of bivalents at meiotic metaphase observed in diploid *Erythrina* species has been reported from many other plant groups. According to a theory introduced by Darlington (1930) and amplified by Lawrence (1931), secondary pairing is due to attraction of homologous or homeologous chromosomes when the degree of homology is not close enough to result in synaptic pairing, and is presumed to be indicative of allopolyploidy. In a recently formed autotetraploid, homology between the two pairs of chromosomes will be nearly complete and a multivalent will be formed at pachytene. In an allotetraploid or in an "old" tetraploid in which the genes of homeologous chromosomes have diverged to some extent, two bivalents result; they may later form a secondary association at metaphase I or late diakinesis due to attraction between the homeologous chromosomes making up the two bivalents. Secondary pairing does not always occur, however; it is a relatively loose association and does not affect disjunction at anaphase I.

This interpretation of secondary pairing and its relation to allopolyploidy has been borne out by quantitative studies of the spatial distribution at metaphase I of marked homeologous chromosomes in the allohexaploid *Triticum aestivum* (Kempanna & Riley, 1964). In other plant groups such a rigorous quantification of secondary pairing has not been obtained, but a number of workers have in-

ferred a history of polyploidy in groups with meiotic secondary pairing, particularly for those with high chromosome numbers suspected to be paleopolyploids. For example, Venkatasubban (1944), in a cytological study of Bignoniaceae, found a base number of $n = 20$ for the family and a presumed ancestral base number of $x = 10$, since up to 10 "secondarily associated" pairs of bivalents were present at metaphase I in many species. The evidence from secondary pairing is not unequivocal, however; in the case of Bignoniaceae, Goldblatt & Gentry (1979) believed $n = 20$ to be a paleohexaploid of a base number $x = 7$, with aneuploidy from $n = 21$.

Both Sundar Rao (1945) and Mehra (1976) noted secondary pairing in *Erythrina*, and the latter author cited it as evidence for an ancestral lower base number for the genus. On the basis of present knowledge, however, it is not possible to state unequivocally that the observed meiotic patterns in diploid *Erythrina* species are due to secondary pairing of specific homologous or homeologous chromosomes, and not simply to random nonhomologous "stickiness" of chromosomal matrix material. Multivalent formation in *E. amazonica*, a neopolyploid, does appear to be a result of true synaptic pairing of homologous chromosomes.

The hybridization trials carried out in *Erythrina* (described below) reveal a high degree of structural and genic homology in the chromosomes of all species, and it is probable that virtually any *Erythrina* genome can combine with that on the same ploidy level of any other species in the genus to form a viable F_1 hybrid. Whether tetraploid *E. amazonica* is of autoploid or alloploid origin, then, it must have two highly homologous sets of chromosomes. It is somewhat surprising that more than two quadrivalents are not usually formed in meiosis I of *E. amazonica*. It is possible that the species contains a specific gene that suppresses multivalent formation and promotes strict homologous pairing of bivalents, similar to the Ph gene which performs this function in hexaploid *Triticum aestivum* (Riley & Chapman, 1958).

Section 4. Experimental Hybridization and Self-Compatibility

Materials and Methods

Experimental hybridizations and self-compatibility trials were conducted at Pacific Tropical Botanical Garden and Waimea Arboretum February–July 1982 and February–April 1984. Although the living *Erythrina* collections at the two gardens share many accessions from the same sources, the species complement of mature, flowering individuals was different at each garden. The use of both gardens allowed a broader inclusion of taxa in the experimental studies than would have been possible otherwise.

In addition, self-compatibility trials and interspecific hybridizations were conducted with natural populations of *Erythrina chiapasana* and *E. goldmanii* at El Sumidero Canyon National Park in Chiapas, Mexico in February 1983. The two species are parapatric at El Sumidero and hybridize naturally (this paper, Section 6).

In all, 32 species were used in the interspecific hybridization trials, in 155 hybrid combinations including reciprocals. Species from throughout the worldwide distribution of *Erythrina* were used in the trials; four of the five subgenera and 12 of the 27 sections were represented. The monotypic African subg. *Tripterolobus* was the only subgenus not included. Eighteen species were tested for self-compatibility. All species used in the trials are diploids ($n = 21$) except *E. amazonica*, a tetraploid ($n = 42$). Attempts were made to hybridize *E. amazonica* as the pollen parent with several diploid species.

The hybrid combinations were selected to represent different "taxonomic distances" between the female and male parental species: "narrow hybridizations" between species of the same section, "medium hybridizations" between species of different sections in the same subgenus, and "wide hybridizations" between species of different subgenera. The narrow hybridizations involved mostly species within sect. *Erythrina*. The medium and wide hybridizations included crosses of sect. *Erythrina* to other sections and subgenera, as well as representative hybridizations not involving sect. *Erythrina*, selected to include the maximum taxonomic diversity and geographic range of the genus.

Constraints on the Experimental Protocol. Shortly after the initiation of the pollination trials, certain constraints imposed by *Erythrina* breeding systems became apparent. Other constraints were imposed by the fact that the experimental subjects were trees exposed to the vicissitudes of the weather and to local, uncontrolled variation in other factors that may affect reproductive success, such as soil fertility and moisture, and insolation. These considerations required a somewhat different experimental protocol and a different statistical treatment of the results than has been customary with biosystematic studies of greenhouse-grown herbaceous plants.

The proportion of fruit set in intraspecific and interspecific pollinations was quite low (see Results, below) and the incidence of postfertilization abortion of young fruits was very high. Pollination success and fecundity varied greatly among individuals of the same species. Some trees were effectively "female sterile": they produced no fruits either spontaneously (i.e., from "open-pollinated" flowers) or from controlled pollinations. At the same time, conspecifics and even individuals from the same accession, which were presumably at least half-siblings of the "female sterile" individuals, produced fruits spontaneously in abundance and produced fruits quite readily from both intraspecific and interspecific controlled pollinations. For many species only a single tree was available, so the use of intraspecific outcrossing success rate as a control was not possible for those species.

Another constraint was the often limited number of flowers per tree that were accessible each day. On many trees only one or a few inflorescences producing three or four new flowers each day were accessible for hand-pollination. The time required to emasculate, isolate, and pollinate each flower individually also limited the number of flowers that could be treated each day. Another practical consideration was the amount of land and labor required for growing the hybrid progeny at the Hawaiian botanical gardens. It was desirable to obtain progeny of many different hybrid combinations, so with limited resources large F_1 families of any particular combination could not be accommodated.

One positive aspect of *Erythrina* reproductive systems that influenced the experimental protocol was the relatively high viability of the seed. Among the hybrids, 45% of the seeds germinated and produced healthy F_1 plants. This high viability meant that large seed lots of any particular combination were not necessary to ensure that at least some progeny would survive to maturity.

The above considerations and constraints led to the development of procedures designed to maximize the number of "narrow," "medium," and "wide" hybrid combinations without undue emphasis on any particular combination. Once several well-formed maturing fruits were produced for any combination, pollinations of that combination were ceased and new combinations were attempted. When possible, species combinations were repeated using several different individuals as female and/or male parents. For self-compatibility trials as well, pollinations within an individual were terminated once several semimature fruits had developed.

In the course of the pollination trials it soon became apparent that certain individual trees of several species were more fecund, successful female parents than others. To the extent possible, pollination trials were concentrated on the more successful females, within the limitations imposed by the number of flowers available. Hybrid combinations or self-pollinations that failed to set fruit were repeated up to 50 times or more, but for many combinations fewer than 10 flowers were pollinated due to limitations of time and available flowers.

Pollination Techniques: Hybridization. The development of suitable techniques to emasculate, isolate, and pollinate the flowers involved considerable trial and error. Nylon mesh bags of several types were used initially to isolate the flowers, but these proved to be too unwieldy, requiring elaborate, heavy wire frames or other means of support so the mesh did not touch the flowers. Also, in rainy weather the high humidity within the mesh bags tended to cause all the flowers to abort.

A simple alternative technique that proved successful was to isolate each flower individually. Floral buds were emasculated at the latest possible stage of development, i.e., on the day before anthesis and pollen release. The tightly closed corolla standard was carefully peeled open, and the anthers were excised with dissecting scissors sterilized in 95% ethanol between each emasculation. If an anther released pollen before removal, the flower was not used in the experiment. Following emasculation, the corolla standard was folded back over the pistil and sealed with plastic Scotch tape. This effectively protected the stigma from any chance pollen deposition and also prevented it from drying out. The following day the corolla was reopened and the standard excised. After pollination a small cone of aluminum foil, formed over the point of a pencil, was placed over the stigma and pinched lightly onto the style. This helped to hold the pollen on the stigma in the face of rain and wind, and isolated the stigma from any other pollen deposition. The cap remained on the stigma throughout the development of the fruit.

For the open-corolla, homogamous species of *Erythrina* adapted to pollination by passerine birds, this technique ensured that the pollen was applied while the stigma was receptive. In most species receptivity was signalled by presence of a wet, sticky exudate on the stigmatic surface on the day of anthesis. For the closed-corolla, protandrous species (primarily sect. *Erythrina*) adapted to hummingbird pollination, the style had not elongated fully and the stigma was not yet receptive on the

day following emasculation. The stigma was thus pollinated prematurely by this method, but the pollen held in place by the aluminum cap evidently remained viable at least until the next day when the stigma became receptive, and these species did set fruit with premature pollination. An alternative method, to wait two days following emasculation to pollinate the protandrous species, yielded no better results and was logistically more complicated.

Stephenson (1981) presented evidence from an extensive literature review that in many plant species, particularly massively blooming trees, only a small fraction of pollinated flowers produce mature fruits; the majority are aborted at an early stage of growth before large amounts of nutrients are channelled into them. The number of fruits that can be matured is usually limited by resource availability, not by pollination. Furthermore, flower and fruit abortion is selective: some species selectively shed self-pollinated flowers. They mature fruits from self-pollinated flowers only when fruit set is low and/or when "higher quality" fruits from cross-pollinated flowers are removed. Therefore there may be "mate competition" within a plant among fruits of different paternity.

In this study attempts were made to reduce, to the extent practical, the effects of resource limitation and competition on mating success. All flowers except the hand-pollinated ones were removed from the inflorescence. Once a few fruits were set on an inflorescence, all flower buds were removed. Until fruits were set, buds were left to develop into flowers available for further pollination trials. Most inflorescences bloomed continuously for several weeks, producing a few new flowers each day, so failed matings could be attempted repeatedly.

An individual inflorescence was treated with pollen from a single source. This eliminated mate competition among the flowers within the inflorescence. An individual tree often had several inflorescences, each pollinated with a different species of male parent, so there could have been interinflorescence competition among mates.

To further reduce resource competition and channel available nutrients into the hand-pollinated flowers, most untreated inflorescences and spontaneous, open-pollinated fruits (those accessible with clipper poles) were removed from the crowns of the trees.

In all species, seeds matured approximately 60 days after pollination. At maturity the hybrid fruit was removed and the number of mature seeds, aborted seeds, and undeveloped ovules was recorded. Length and width of each mature seed were measured for comparison with seeds produced from intraspecific matings.

Tests for Self-Compatibility, Autogamy, and Apomixis. For self-pollinations and intraspecific outcrosses, anthers were not emasculated, but the corolla standard of the flower bud was sealed with tape prior to dehiscence to prevent chance deposition of nonself pollen on the stigma. When the stigma became receptive, pollen from the same tree (for selfs) or from different conspecific trees (for outcrosses) was applied, and a cap of aluminum foil was placed over the stigmas in the same manner as in the intraspecific hybridizations.

The pollen for the outcrosses was a mixture from all available conspecific trees in the botanical garden, including individuals from the same accession as the female parent as well as from different accessions. For the self-compatibility trials carried out in the natural populations of *Erythrina chiapasana* and *E. goldmanii* at El Sumidero, the pollen for the outcrosses was a mixture of at least five different individuals in the population.

The treated flowers of an individual inflorescence were either all selfed or all outcrossed to eliminate within-inflorescence mate competition.

The abortion of young fruits during the first two to three weeks following fertilization was very high for selfs and intraspecific outcrosses, as well as for interspecific hybridizations. Fruit set data were taken at least four weeks following pollination, after which abortion of the developing fruits was negligible. Complete data on intraspecific reproductive success, including mature seed production and seed size, germination success, and viability of the progeny, were obtained only for cultivated *Erythrina guatemalensis* and *E. crista-galli.* Several individuals of these species from different accessions were available for the trials, and they were the most successful female parents in the interspecific hybridizations. For comparative analyses, then, the intraspecific data were particularly desirable for these two species. Because of space and labor limitations, intraspecific progeny could not be raised for all species.

In the flowers of sect. *Erythrina* and the other hummingbird-pollinated sections of the genus, the anthers and stigma are positioned close to one another. Initial observations indicated that, although the flowers are protandrous, autogamy may sometimes take place. Autogamy was tested by isolating entire inflorescences in wire-framed nylon mesh bags. After all the flowers had either aborted or set fruit, the mesh was removed. Six species were tested this way at Pacific Tropical Botanical

Garden during a period of relatively dry weather (May 1982) to minimize abortion of flowers caused by high humidity inside the mesh bags.

Autogamous fruits were obtained only on the most distal flowers (the last to open) on inflorescences of two individuals of *Erythrina guatemalensis* (Results, Table 4). These individuals were tested for agamospermy. On three inflorescences of each plant, all the flowers on the distal one-third of the inflorescence were emasculated before dehiscence, and the stigmas were covered with aluminum foil caps to prevent any pollen deposition on the stigma. Fruit set was monitored in the same manner as in the pollination trials.

Statistical Analysis of Results. The protocol described above was necessitated by the flowering patterns and reproductive traits of *Erythrina*, by practical limitations of breeding trees in the heterogeneous environments of open-air botanical gardens, and by the goal of obtaining viable progeny of as many "narrow," "medium," and "wide" hybrid combinations as possible. The resulting small and very unequal sample sizes for different hybrid combinations as well as for selfings and intraspecific outcrosses meant that outcomes of particular combinations could not be compared statistically. Instead, for statistical analyses hybrid combinations and intraspecific matings were pooled into broad categories based on taxonomic distance (assumed for the purposes of the study to be a true representation of relative genetic and phylogenetic distance) between the female and male parents. The five experimental treatments are: self-matings, intraspecific outcrosses, and the three categories of hybrid combinations—"narrow," "medium," and "wide" hybridizations.

For statistical analyses, mating success for each treatment was expressed as the proportion of hand-pollinated flowers producing mature fruit (i.e., a fruit with at least one fully developed, normal-sized seed). The commonly used analysis-of-variance (ANOVA) tests (e.g., Sokal & Rohlf, 1969; Statistical Analysis Institute, 1982) are designed to test the significance of differences between means of continuously variable data. ANOVA tests are inappropriate for categorical (either/or) data, such as mating success, where the outcome of a pollination attempt falls into one of only two categories. A multiple comparison test for differences between proportions, appropriate for categorical data, was devised by Alan R. Templeton for these analyses. Templeton's test allows for pairwise comparisons of all combinations of the five treatment categories; also, categories can be pooled to test various hypotheses regarding mating success (e.g., all intraspecific vs. all interspecific matings).

The null hypothesis for the test was that there is no difference in proportion of mature fruits produced among any of the pollination treatments. This is a corollary of the central hypothesis of this research: that there are no interspecific or self-incompatibility barriers to mating within *Erythrina*, that any pair of gametes from any species in the genus are equally likely to pair successfully, form a viable zygote, and grow into a healthy adult sporophyte regardless of the infrageneric taxonomic position or putative phylogenetic distance between the parents.

Templeton's test is an inequality that compares the differences between proportions with their variances. Proportions are subjected to an arcsine–square root transformation to set the variance independent of the mean; the variance is inversely proportional to the sample size. The 95% confidence limits of the proportion are:

$$X = \arcsin \sqrt{\frac{F}{N}} \pm 1.96 \sqrt{\frac{1}{4N}},$$

where F = number of mature fruits (successful matings); N = number of flowers pollinated (attempted matings).

For small sample sizes ($N < 50$), the arcsine–square root transformation is corrected:

$$X = \frac{1}{2}\left(\arcsin \sqrt{\frac{F}{N+1}} + \arcsin \sqrt{\frac{F+1}{N+1}}\right).$$

For the general case, the null hypothesis is rejected at $P = 0.05$ if the inequality is true:

$$\left|\sum a_i X_i\right| > 0.98 \sqrt{\frac{a_i^2}{N_i}},$$

where X_i = the arcsine–square root transformed proportion of successful matings in the ith category; N_i = sample size (total number of flowers pollinated in the ith category); and a_i = a weighting factor set so that $|\sum a_i| = 0$.

The a_i for each category is proportional to the sample size N_i.

For pairwise comparisons between categories i and j, the inequality is simplified; the H_0 is rejected at $P = 0.05$ if it is true that

$$|X_i - X_j| > 0.98 \sqrt{\frac{1}{N_i} + \frac{1}{N_j}}.$$

For a test of "highly significant" difference at

$P = 0.01$, the term "0.98" on the right side of the inequality is replaced by the value "1.28."

Several individuals of *Erythrina guatemalensis* and *E. crista-galli* were the most fecund, successful females in the interspecific hybridizations as well as the intraspecific matings. For all categories employing these two species as female parents, separate multiple comparison tests were used to compare mating success. These comparisons included both selfings and intraspecific outcrosses for *E. guatemalensis* but only selfings for *E. crista-galli*, which had only one individual in flower at each garden (Pacific Tropical and Waimea) when the pollinations were conducted.

Separate statistical tests were carried out for the self-compatibility trials of individual species. For those species with analyzable data on fruit set of self-pollinations vs. intraspecific outcrosses, the data were ordered into 2 × 2 contingency tables. With small sample sizes and values of less than 5 in many cells of the contingency tables, the standard chi-square test was not appropriate; so Fisher's exact probability was computed for the outcomes (Sokal & Rohlf, 1969). For the pooled self-compatibility data including all species tested, the sample size was large enough for a chi-square test.

F_1 Hybrid Viability. The F_1 hybrid seeds were planted within a few weeks after harvest. To the extent possible, seed lots of each hybrid combination were divided for propagation at two sites. The F_1 plants were raised by the horticulturists at Pacific Tropical and Ho'omaluhia Botanical Gardens, who monitored germination success, growth, and vigor of the hybrids. Evaluations were made approximately once each six months using a standardized form. Survivorship, growth rates, and indications of chlorosis or other abnormalities were recorded.

The multiple comparison test described above for analysis of fruit set was employed for a statistical evaluation of hybrid viability, defined as the proportion of seeds in each category that germinated and survived as healthy plants for six months (after which mortality in the garden was negligible). Viability of the "narrow," "medium," and "wide" F_1 hybrids was compared, together with that of the "narrow" F_2 hybrids in sect. *Erythrina* (see below). Seeds from controlled intraspecific matings of *Erythrina guatemalensis* and *E. crista-galli* were planted along with the hybrids. For each of these species a separate multiple comparison test was conducted for viability of "intraspecific" seed vs. hybrid seed having these two species as female parents.

F_1 Hybrid Fertility. Many of the narrow hybrids between species in sect. *Erythrina*, produced in 1982, grew to be 4-m trees and produced flowers by February 1984. By several different measures of fertility, these F_1s were compared with the parental species and their meiosis examined. As an estimate of pollen fertility, percentage of stainable (nonaborted) pollen was determined for the F_1 hybrids and their parents using Alexander's double stain technique (Alexander, 1969) (at least 500 grains counted per sample) and compared with a one-tail *t*-test.

Fecundity of F_1 Hybrids. As discussed earlier, one goal of the hybridization study was to assess the relative fitness of the hybrids in comparison with their parents. The viability, vigor, meiotic regularity, and pollen fertility of the hybrids are indicators of fitness, but a more direct measure is their relative reproductive success vis-à-vis that of the parental species. During the period of this study the F_1 hybrids, although some of them produced flowers and fruits, did not grow into full-sized adult trees, so a thorough assessment of hybrid fecundity and fitness was not possible. However, a preliminary indication of reproductive success was obtained from the two-year-old narrow hybrids in sect. *Erythrina* that flowered in the spring of 1984.

Controlled self-pollination of some of these F_1 hybrids was conducted in order to obtain seed for a limited number of F_2 families. The multiple comparison test was employed for pairwise comparisons of mating success (proportion of hand-pollinated flowers producing mature fruits) between the selfed F_1s and their parental species. Different categories of parental matings varied among themselves in mating success, and several types of parental matings were compared with the selfed F_1s. The pairwise comparisons of fruit set included: 1) selfed F_1s vs. their own parental matings, i.e., the original hybridizations that produced the F_1s used in the trials; 2) selfed F_1s vs. all paired combinations of the parental species, including the reciprocals that failed to produce F_1 hybrids; 3) selfed F_1s vs. selfed parental species. The logic for using these particular groupings of parental matings in the comparative assessment of F_1 reproductive success is discussed in the Results.

Viability of F_2 Hybrids. Many of the F_1s also produced fruit and mature seed spontaneously on open-pollinated inflorescences, almost certainly the result of autogamy. F_2 seed lots from selfed flowers, and some from open-pollinated flowers, were planted along with the 1984 F_1 hybrids. The viability

of the F_2 progeny was compared with that of the F_1s.

Studies of Previously Synthesized Hybrids. A few *Erythrina* hybrids have been produced in the past by horticulturists and are commonly grown in tropical and subtropical regions. Two were available at the Hawaiian gardens: *Erythrina* ×*bidwillii* and *E.* ×*sykesii*. Studies of meiosis, pollen fertility, and fruit set from controlled self-pollinations were conducted on these plants with the methods described above.

Hybrid Names. In this paper horticultural convention (Brickell et al., 1980) is followed for the hybrid names. For artificial hybrids when the female parent is known, the female parent is first in the hybrid formula name. When the female parent is not known, as in natural hybrids, the order of the constituent species names is alphabetical.

RESULTS AND DISCUSSION

The results of the experimental hybridizations, self-compatibility trials, and studies of viability and fertility of the progeny are presented in summary form for the statistical analyses of the data. In addition, more complete data sets, listing the results obtained from individual plants, are presented in certain of the tables below.

There are several reasons for this more thorough reporting of the data. The first is to provide the most complete information available on the ancestry of each individual in the F_1 and subsequent hybrid generations. The full documentation is necessary for the studies on the inheritance of various traits in the hybrids. Studies of morphological inheritance were initiated in this paper (Section 5), and research on the inheritance of micromolecular and macromolecular traits in the interspecific hybrids is anticipated for the future. In addition, some of the hybrid plants with their colorful flowers are likely to be propagated widely as ornamentals; the tables presented here serve as public documentation of the parentage of these cultivars. Finally, it is hoped that some of these experiments will be repeated with the same parental and hybrid trees in the Hawaiian botanical gardens. The documentation of the results for individual plants of traits probably indicative of reproductive success, such as pollen fertility and fruit set, will allow investigation of the possibility that such traits may change through time with the maturation of the plant.

Self-Compatibility. The results of the self-compatibility trials are shown in Table 3. The low percentage of mating success in the pooled data for all species—6% fruit set for selfings and 10% for outcrosses—is due to a high incidence of postzygotic abortion of young fruits and to failure of pollen tubes to reach the ovules, but the relative importance of these two factors is not known. For the pooled totals, the difference in fruit set between selfs and outcrosses is nonsignificant.

Statistical comparison of fruit set in selfs vs. outcrosses was possible in four species. In only one of these, the natural population of *Erythrina goldmanii* at El Sumidero, was fruit set significantly higher in outcrosses than in selfs, and then but marginally so at $P = 0.05$.

In six additional species, self-pollinated flowers set fruit, but only one individual of the species was available, so the outcrossing control was not possible. In nine species, no fruits were set from self-pollinated flowers, but in four of these the outcrossing controls yielded no fruits either. Failure of fruit set, then, is evidently a consequence of overall low fecundity in *Erythrina* and not of self-incompatibility per se.

Self-incompatibility has previously been reported for seven species of *Erythrina*: *E. senegalensis* and *E. speciosa* (East, 1940); *E. crista-galli* (Fryxell, 1957); *E. mitis* and *E. poeppigiana* (Arroyo, 1981); *E. leptorhiza* (Hernández & Toledo, 1979); and *E. montana* (Hernández, 1982). Only for *E. montana* was the assertion of self-incompatibility supported by evidence from experimental self-pollinations and outcrossing controls. Calculation of Fisher's exact probability for the data presented in Hernández (1982), however, reveals that the difference in fruit set between selfs and outcrosses in *E. montana* is nonsignificant ($P = 0.25$). My evidence for self-compatibility in *E. senegalensis* and *E. crista-galli* contradicts the earlier reports of self-incompatibility in these species, which were based merely on the failure of isolated cultivated trees to produce seed spontaneously. Feinsinger et al. (1979) provided evidence from experimentally controlled pollinations that *E. fusca* and *E. pallida* are self-compatible.

There is thus no reliable evidence for genetic self-incompatibility in any species of *Erythrina*. It appears safe to assume that genetic self-incompatibility—at least the classical single-locus, multiple S-allele, stigma- or style-mediated model of self-incompatibility (Nettancourt, 1977)—is completely absent from the 112 species in the genus. If this is true, it would invalidate some of the evidence that Arroyo (1981) advanced to support her assertion that tropical woody Papilionoideae are predominantly self-incompatible. Five of the

TABLE 3. *Self-compatibility trials in* Erythrina.

Species[1]	Self		Outcross		Probability, Self vs. Cross
	Flowers	Fruits[2]	Flowers	Fruits[2]	
E. berteroana (4)	27	0	9	0	—
E. chiapasana (2)	14	0	—	—	—
E. chiapasana[3] (6)	32	4 (0.13)	15	1 (0.07)	0.48*
E. crista-galli (1)	27	7 (0.26)	—	—	—
E. elenae (1)	27	0	—	—	—
E. falcata (1)	5	1 (0.20)	—	—	—
E. folkersii (1)	2	2 (1.0)	—	—	—
E. fusca (2)	82	1 (0.01)	85	1 (0.01)	> 0.05**
E. goldmanii[3] (6)	27	3 (0.11)	23	8 (0.35)	0.05*
E. guatemalensis (5)	33	3 (0.09)	28	7 (0.25)	0.09*
E. latissima (1)	10	0	—	—	—
E. lysistemon (1)	25	4 (0.16)	—	—	—
E. perrieri (2)	27	0	1	0	—
E. sandwicensis (1)	49	2 (0.04)	—	—	—
E. senegalensis (1)	28	2 (0.07)	—	—	—
E. speciosa (2)	21	0	8	0	—
E. standleyana (1)	9	0	—	—	—
E. tahitensis (2)	64	0	—	—	—
E. variegata (1)	6	0	6	0	—
Total	515	29 (0.06)	175	17 (0.10)	> 0.05**

[1] In parentheses: number of individuals used in trials.
[2] In parentheses: proportion of pollinated flowers producing mature fruits.
[3] Pollinations conducted in natural population at El Sumidero, Chiapas, Mexico.
* Fisher's exact probability.
** Chi-square probability.

27 species Arroyo listed in that habitat/life form category as self-incompatible were *Erythrina* species. There are very few comparable studies on other genera of tropical woody Papilionoideae. With the information presently available, it is not known if *Erythrina* is an anomaly, or if self-compatibility is common in this group of plants. Because low fecundity and high rates of flower and fruit abortion are probably characteristic of these plants, greater caution is required in carrying out and interpreting self-incompatibility tests than has customarily been taken.

It is true that fruit set is frequently lower in self-matings than in outcrosses. This may be due not to genetic self-incompatibility, but rather to multiallelic inbreeding depression, expressed either in the progamic phase as failure of pollen tubes to reach the ovules (Mulcahy & Mulcahy, 1983) or as postzygotic abortion of young fruits.

Although *Erythrina* species are genetically self-compatible, the production of seed from selfed flowers in natural populations may be quite limited. A flowering tree visited by pollen-bearing birds will receive many geitonogamous pollinations (pollen from a different flower on the same individual) as well as xenogamous pollinations (pollen from a different individual). The reduced fruit production from self-pollinations, as well as the relatively poor viability of selfed seed (see section on F_1 viability below) suggests that progeny derived from selfed flowers are low in "quality" relative to progeny derived from outcrossed flowers. The selective abortion of low-quality selfed fruits, cited by Stephenson (1981), may be operative in *Erythrina*. Interfruit competition may be very intense under natural conditions, since such a small proportion of pollinated flowers develops into mature fruits. Therefore it is possible that most successful progeny are derived from outcrossing, and that the level of inbreeding in most *Erythrina* populations is quite low in spite of self-compatibility and a large proportion of geitonogamous pollinations. This is still speculative; the significance to mating success of mate competition among male parents has not been explored in *Erythrina*.

In regard to flower and fruit abortion, the attempts to increase mating success by eliminating the effects of competition and resource limitation in the experimental pollination trials were only partially successful. Certainly the fruit maturation rates of 25% or more obtained in some of the outcrossing trials represent an increase in fruit production over

TABLE 4. *Tests for autogamy and agamospermy in* Erythrina *at Pacific Tropical Botanical Garden.*

I. Test for autogamy

Species	Accession Number	Inflorescences Bagged	Flowers	Fruits	Seeds
E. abyssinica	770034001	3	90	0	0
E. berteroana	700044001	3	124	0	0
E. crista-galli	740283001	3	152	0	0
E. guatemalensis	720999001	2	165	1	2
E. guatemalensis	720999002	3	96	0	0
E. guatemalensis	750419001	3	148	5	8
E. humeana	740283001	4	156	0	0
E. macrophylla	750420001	4	86	0	0
E. salviiflora	721000002	2	63	0	0

II. Test for agamospermy (in individuals exhibiting autogamy)

Species	Accession Number	Inflorescences Treated	Flowers Emasculated	Fruits Set
E. guatemalensis	750419001	3	30	0
E. guatemalensis	720999001	3	66	0

the percentages found in natural populations. Usually the percentages of fruit maturation were much lower, however, and in all cases the majority of pollinated flowers were aborted early in development. The factors promoting flower and fruit abortion are several, including nutrition and resource limitation, competitive effects, possible damage to the flowers caused by emasculation, and factors such as adverse weather conditions, in addition to the factor under consideration here: the genetic compatibility of the female and male parents. Neither for the self-compatibility trials nor for the experimental hybridizations was it possible to sort out all of these variables.

Autogamy and Agamospermy. The results of the tests for autogamy and agamospermy are shown in Table 4. Autogamous fruits were produced only on two individuals of *Erythrina guatemalensis*. Significantly, these were rather "fecund" trees with relatively high mating success from controlled hand-pollinations. The autogamous fruits were produced only from the uppermost three fascicles of flowers on an inflorescence—the last flowers to bloom. They evidently were produced, in part, because of the occasional breakdown of protandry, which prevents autogamy on most flowers of *E. guatemalensis* and the other species that are adapted to hummingbird pollination (Neill, 1987).

Although autogamous fruits were produced in my limited trials only on *Erythrina guatemalensis*, I believe that occasional autogamy is widespread in the genus. Cultivated trees of many species produce some fruits spontaneously in the absence of evident pollen vectors.

The fact that autogamous fruits are produced only on the latest flowers of an inflorescence suggests that the breakdown of protandry may be an adaptive mechanism that allows some seed set in the absence of the appropriate avian pollen vectors. Each inflorescence, although it may produce 75 or more flowers, will mature only a few fruits, so fruit set on the lower, earlier-blooming flowers of the inflorescence must inhibit the formation of fruits on the upper, later-blooming portion. It is likely that autogamous fruits from the ultimate flowers of the inflorescence will be produced only if some allogamous fruits (from either xenogamous or geitonogamous pollinations) have not already been produced on the lower portion of the inflorescence.

The two *Erythrina guatemalensis* trees that produced autogamous fruits were tested for agamospermy (Table 4). No fruits were produced when stigmas were isolated from pollen deposition, so agamospermy is not indicated. Agamospermy is almost unknown in the Leguminosae (Arroyo, 1981) and it is unlikely to occur in *Erythrina*.

Hybridization Trials: Mating Success (Fruit Maturation). The complete results of the hybridization trials are listed in Appendix II. From 1,671 hybridization attempts in 155 hybrid combinations, 98 mature fruits were produced in 47 hybrid combinations, for an overall hybrid mating success of 6%, in 30% of the attempted combinations.

TABLE 5. *Proportion of hand-pollinated flowers producing mature fruit: all diploid* Erythrina *species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	515	29	5.6%
Intraspecific outcross	175	17	9.7%
Narrow hybridization (within section)	540	50	9.3%
Medium hybridization (between sections, within subgenus)	350	22	6.3%
Wide hybridization (between subgenera)	705	25	3.6%
Total	2,285	143	6.3%

Multiple comparison test for differences between treatments in proportion of fruit set

Self vs. outcross	N.S.[1]
Self vs. narrow hybrid	$P < 0.05$
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium hybrid	N.S.
Outcross vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	$P < 0.01$
Medium hybrid vs. wide hybrid	N.S.
Intraspecific vs. hybrids	N.S.
Outcross + narrow hybrids vs. self + medium + wide	$P < 0.01$

[1] N.S. = not significant ($P > 0.05$).

For the statistical analysis of mating success in selfs, intraspecific outcrosses, and hybridizations (Table 5), data from the diploid species only were included. The tetrapoloid *Erythrina amazonica* as male parent, after numerous pollination attempts with the diploids *E. guatemalensis* and *E. cristagalli* as female parents, produced one hybrid seed with each of the females. Neither of the seeds germinated, however, so there are no successful hybrids between *Erythrina* species of different ploidy levels. Since the results from *E. amazonica* are not germane to the hypotheses of the interfertility of diploid species and the formation of homogamic complexes, they were excluded from the statistical analysis.

The results for the diploid species in Table 5 indicate that the highest mating success was obtained with intraspecific outcrosses and "narrow" hybridizations (within sections). "Medium" hybridizations (intersectional, intrasubgeneric) and selfings were intermediate in mating success, and "wide" (intersubgeneric) hybrids were the least successful of the five treatment classes. A general trend, then, is evident: interspecific matings between closely related species (within sections) are just as likely to succeed as intraspecific matings. Mating success diminishes with increasing "taxonomic distance" between the parents (intersectional and intersubgeneric hybridizations). Mating success is also somewhat lower in selfings than either intraspecific outcrosses or hybridizations between closely related species.

This overall trend, shown by the percentages of fruit maturation in Table 5, is not a strong one; the differences between treatments are for the most part nonsignificant. The multiple comparison test revealed only three significant differences among the ten possible pairwise combinations. Fruit maturation in narrow hybridizations was significantly higher than in self-mating ($P < 0.05$). Intraspecific outcrosses and narrow hybridizations also had higher fruit maturation than wide hybridizations; in these comparisons the difference was highly significant ($P < 0.01$).

Because the pooled fruit maturation data for all species may obscure the heterogeneity in results among different species, it is instructive to examine the patterns of mating success in a few selected species. *Erythrina guatemalensis* as female parent accounted for 30% of all mature fruits in the pollination trials and 33% of all the hybrid fruits. Thirty-three hybrid fruits were produced from *E. guatemalensis* as female; of these, 30 (90%) were from a single genetic individual, a clone represented by one tree at each garden (PT 700018001, WA 74c1453). The pattern of mating success for *Erythrina guatemalensis* (Table 6) is very similar to the overall results for the combined species trials.

TABLE 6. *Proportion of hand-pollinated flowers producing mature fruit: female parent* = Erythrina guatemalensis; *male parents = diploid species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	33	3	9%
Intraspecific outcross	28	7	25%
Narrow hybridization (within section)	86	21	24%
Medium hybridization (between sections, within subgenus)	54	5	9%
Wide hybridization (between subgenera)	185	7	4%
Total	386	43	11%

Multiple comparison test for differences between treatments in proportion of fruit set	
Self vs. outcross	N.S.
Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium hybrid	N.S.
Outcross vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	$P < 0.05$
Medium hybrid vs. wide hybrid	N.S.
Outcross + narrow hybrid vs. self + medium + wide	$P < 0.01$

The *E. guatemalensis* trees were unusually fecund; fruit maturation was much higher than the overall average for intraspecific outcrosses (25%) and narrow hybridizations (24%). As in the combined species results, fruit maturation was significiantly higher in intraspecific outcrosses and narrow hybridizations than in wide hybridizations ($P < 0.01$ for both pairwise comparisons), and for narrow hybridizations vs. medium hybridizations the difference was marginally significant ($P < 0.05$).

The data set for *Erythrina crista-galli* as female parent (Table 7), although not so extensive, shows that the neat congruence of mating success and taxonomic distance evidenced by *E. guatemalensis* does not always apply. *Erthyrina crista-galli* as female, represented by one genetic individual at each of the two gardens, produced 16% of all the hybrid fruits in the trials, but it produced 49% of the "medium" and "wide" hybrid fruits. Fruit maturation was higher in the medium and wide hybridizations than in the few narrow hybridizations. (Only one species, *Erythrina falcata*, is in the same section with *E. crista-galli*, so the opportunities for narrow hybridization were limited.) There are no significant differences, however, in any of the pairwise comparisons between pollination treatments for *E. crista-galli*; the variances are large because the sample sizes are rather small.

For intersectional hybridizations (the "medium" and "wide" categories combined) mating success in *Erythrina crista-galli* as female parent was significantly higher than in *E. guatemalensis* (multiple comparison test for proportions, $P < 0.05$). This is illustrated by the results of attempted reciprocal hybridizations between these two species, which are in different subgenera. Sixty-four pollination attempts to produce the hybrid *E. guatemalensis* ♀ × *E. crista-galli* ♂ yielded a single fruit with two seeds, neither of which germinated. Only ten attempts at the reciprocal cross of *E. crista-galli* ♀ × *E. guatemalensis* ♂ yielded four fruits, 15 seeds, and eight vigorous F_1 plants. In all, *E. crista-galli* as female parent produced seeds from seven hybrid combinations with species in six sections and three subgenera. Five of these combinations in all three subgenera survived as healthy F_1 plants. *Erythrina crista-galli*, in short, was a singularly successful "wide hybridizer."

Summing up the contrasting results in fruit maturation for *Erythrina guatemalensis* and *E. crista-galli*, *E. guatemalensis* hybridized very readily with species in the same section, much less so with more distantly related species. *Erythrina crista-galli*, in contrast, hybridized with a number of species in different subgenera with apparently equal facility, regardless of the formal taxonomic relationships and presumed phylogenetic affinities between *E. crista-galli* and the male parents. These

TABLE 7. *Proportion of hand-pollinated flowers producing mature fruit: female parent* = Erythrina crista-galli; *male parents = diploid species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	27	7	26%
Narrow hybridization (within section)	22	2	9%
Medium hybridization (between sections, within subgenus)	69	11	16%
Wide hybridization (between subgenera)	64	10	16%
Total	182	30	16%

Multiple comparison test for differences between treatments in proportion of fruit set

Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	N.S.
Medium hybrid vs. wide hybrid	N.S.

differences in mating success probably reflect individual variation rather than real and consistent interspecific differences in crossability.

F_1 Hybrid Viability. Viability of the F_1 hybrids was high and equal to or higher than normal viability of progeny within species. Overall, 143 (52%) of the 273 F_1 hybrid seeds germinated; 120 of these (44% of the total) survived as healthy F_1 plants. In other words, most of the F_1 seeds either germinated and grew vigorously or they did not germinate at all: the survival rate of those that germinated was 84%.

There were few instances of weakness in the hybrids. Two individuals completely lacked chloroplasts and died soon after germination: a narrow hybrid, *Erythrina macrophylla* × *E. berteroana*, and a wide hybrid, *E. crista-galli* × *E. speciosa*. In both cases, though, siblings from the same cross grew into healthy green plants. About 10 other hybrid plants in different combinations were chlorotic, with yellow-green foliage, and died within 1–2 months. Several others at first appeared chlorotic, but after several months they recovered the normal green color and grew vigorously.

The comparative viablity of narrow, medium, and wide hybrids is summarized in Table 8. Among the F_1 hybrids viability (defined as successful germination and survival of the plant for at least six months) was highest for narrow hybrids, intermediate for wide hybrids, and lowest for medium hybrids. The difference between viability of narrow and medium hybrids was statistically significant ($P < 0.01$), but between narrow and wide hybrids it was not.

TABLE 8. *Viability of hybrid* Erythrina: *proportions of seeds germinating and growing into healthy plants (at 6 months).*

Type of Hybrid Seed	Seeds Sown	Live Plants	Proportion Viability
Narrow F_1 hybrid	167	86	51%
Narrow F_2 hybrid (all within sect. *Erythrina*)	66	7	11%
Medium F_1 hybrid	62	16	26%
Wide F_1 hybrid	44	18	41%
Total	339	127	37%

Multiple comparison test for differences in viability between types of hybrid

F_1 narrow vs. F_2 narrow	$P < 0.01$
F_1 narrow vs. F_1 medium	$P < 0.01$
F_1 narrow vs. F_1 wide	N.S.
F_2 narrow vs. F_1 medium	N.S.
F_2 narrow vs. F_1 wide	$P < 0.01$
F_1 medium vs. F_1 wide	N.S.
All F_1 hybrids vs. F_2 narrow hybrids	$P < 0.01$

Included in Table 8 is the viability data for the "narrow F_2" hybrid seed produced in 1984 from the two-year-old narrow F_1s within sect. *Erythrina*. Germination success of the F_2s was very low, an unexpected and anomalous result; the difference in viability between both the narrow F_1 hybrids (51%) and the wide F_1s (41%) vs. the narrow F_2s (11%) was highly significant (both comparisons, $P < 0.01$).

Viability data for the intraspecific and hybrid progeny of maternal *Erythrina guatemalensis* and *E. crista-galli*, respectively, are presented in Tables 9 and 10. The intraspecific progeny of these two species were grown for two purposes: to compare their viability with that of the hybrids from the same female parents, and to carry out a study of intraspecific variation of morphological traits among siblings. The second goal was thwarted, however, because of the poor germination of the intraspecific seeds. Although the seed lots were not large to begin with, viability of the seed derived from selfings was particularly low: all seven selfed

TABLE 9. *Viability of seed produced from* Erythrina guatemalensis *as female parent (intraspecific and hybrids). Proportion of seed germinating and growing into healthy plants (at 6 months).*

Paternity of Seed	Seeds Sown	Live Plants	Proportion Viability
Selfed	12	1	8%
Intraspecific outcross	14	4	29%
Narrow hybrid (within sect. *Erythrina*)	93	39	42%
Medium and wide hybrids	19	2	11%
Total	138	46	33%

Multiple comparison test for differences in viability between seed of different paternity; female parent = *Erythrina guatemalensis*

Self vs. outcross	N.S.
Self vs. narrow hybrid	$P < 0.05$
Self vs. medium & wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium & wide hybrid	N.S.
Narrow hybrid vs. medium & wide hybrid	$P < 0.01$
Self vs. all hybrids	$P < 0.01$
Outcross + narrow hybrid vs. self + medium + wide hybrids	$P < 0.01$

TABLE 10. *Viability of seed produced from* Erythrina crista-galli *as female parent (selfs and hybrids). Proportion of seeds germinating and growing into healthy plants (at 6 months).*

Paternity of Seed	Seeds Sown	Live Plants	Proportion Viability
Selfed	7	0	0%
Narrow hybrid	4	1	25%
Medium hybrid	33	7	21%
Wide hybrid	24	10	42%
Total	70	18	26%

Multiple comparison test for differences in viability between seed of different paternity; female parent = *Erythrina crista-galli*

Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	$P < 0.01$
Self vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	N.S.
Medium hybrid vs. wide hybrid	N.S.
Self vs. all hybrids	$P < 0.01$

seeds of *E. crista-galli* failed to germinate, as did all but one of 12 selfed seeds of *E. guatemalensis*. This could be an expression of inbreeding depression in the self-progeny, but this possibility must be corroborated with larger samples.

Among the hybrids derived from *Erythrina guatemalensis* and *E. crista-galli* females, the pattern of F_1 viability (Tables 9, 10) and its relationship to "taxonomic distance" between the parents was similar to the pattern of mating success discussed earlier (Tables 6, 7) for the same two species. Among the progeny of *E. guatemalensis*, viability of narrow hybrids was significantly higher than that of medium and wide hybrids. Among the progeny of *E. crista-galli*, by contrast, there was no correlation between F_1 hybrid viability and the degree of relatedness of the parentals.

A complete listing of the F_1 hybrid plants produced during 1982–1984 is contained in Tables 11–13. In all, there are 120 individuals in 33 hybrid combinations (21% of the 155 attempted combinations): 22 narrow hybrid combinations (34% of 65 attempted combinations); four medium hybrid combinations (15% of 27 attempts); and seven wide hybrid combinations (11% of 64 attempts). The number of individual F_1 hybrids for each combination ranges from one to nine.

Nineteen of the 22 narrow hybrid combinations are between species in sect. *Erythrina*. There is one narrow hybrid combination in each of sections *Cristae-galli*, *Chirocalyx*, and *Erythraster*. The medium and wide hybrids include species combinations in nine of the 26 sections of *Erythrina* and four of the five subgenera. In seven of the hybrid combinations, one parental species is native to the New World and the other is native to the Old World.

In summary, the viable F_1 hybrids obtained between the diploid species of *Erythrina* include representative crosses that bridge the entire range of taxonomic diversity and geographic distribution of the genus. Interspecific crossability appears to be largely a function of individual variation in fecundity of the female parent and only partially a function of taxonomic/phylogenetic distance between male and female parents. Given the results obtained in these experiments, it may be expected that with sufficient time, perseverance, and selection of compatible and fecund individual genotypes, any diploid *Erythrina* species could be crossed with any other to produce a viable F_1 hybrid.

Sexual Maturation and Fertility of F_1 Hybrids. Some F_1 hybrids not only were very rapid

TABLE 11. *Artificial* Erythrina *hybrids: narrow (intrasectional).*

Hybrid	Hybrid Number	Live Plants	Hybrid Accession Numbers*	Parental Accession Numbers*
	Sect. *Cristae-galli*			
E. crista-galli × *E. falcata*	2×3-1	1	HO 84.284	PT 740283001 (F) PT 750086001 (M)
	Sect. *Erythrina*			
E. americana × *E. berteroana*	25×53-1	1	PT 820420	WA 75c1171 (F) WA 74s864 (M)
E. berteroana × *E. guatemalensis*	53×43-1	6	HO 82.647 PT 820549	WA 78s564 (F) WA 74c1453 (M)
E. chiapasana × *E. berteroana*	36×53-1	8	HO 82.278 PT 820283	PT 721005001 (F) PT 700044002 (M)
E. goldmanii × *E. chiapasana*	29×36-1	1	WA 84c560	*Neill 5617* (F) *Neill 5497* (M)
E. guatemalensis × *E. berteroana*	43×53-1	2	HO 82.289	PT 700018001 (F) PT 700044001 (M)
E. guatemalensis × *E. berteroana*	43×53-3	6	HO 82.641 PT 820493	PT 750419001 (F) PT 730711001 (M)
E. guatemalensis × *E. berteroana*	43×53-4	1	HO 82.642	PT 720999001 (F) PT 700044001 (M)
E. guatemalensis × *E. chiapasana*	43×36-1	4	HO 82.283 PT 820254	PT 700018001 (F) PT 721005001 (M)
E. guatemalensis × *E. chiapasana*	43×36-2	5	HO 82.284 PT 820278	PT 700018001 (F) PT 730710001 (M)
E. guatemalensis × *E. folkersii*	43×31-1	2	HO 82.282	PT 700018001 (F) PT 700010001 (M)
E. guatemalensis × *E. macrophylla*	43×42-1	4	HO 82.285	PT 700018001 (F) PT 750420002 (M)
E. guatemalensis × *E. macrophylla*	43×42-3	2	PT 820276	PT 750420002 (M)
E. guatemalensis × *E. macrophylla*	43×42-4	2	HO 82.288	PT 750420002 (M)
E. guatemalensis × *E. salviiflora*	43×56-1	1	PT 820492	PT 750419001 (F) PT 721000002 (M)
E. guatemalensis × *E. standleyana*	43×23-3	2	HO 82.765	WA 74c1453 (F) WA 76s1056 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-1	1	HO 82.335	WA 74c1453 (F) WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-4	2	HO 82.640	WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-5	5	PT 820546	WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-6	1	PT 820547	WA 74c1448 (M)
E. herbacea × *E. americana*	22×25-2	2	HO 82.759	WA 75c1103 (F) WA 75c1171 (M)
E. herbacea × *E. berteroana*	22×53-1	1	PT 820541	WA 75c1103 (F) WA 74s864 (M)
E. herbacea × *E. guatemalensis*	22×43-1	2	PT 820421	WA 75c1103 (F) WA 74c1453 (M)
E. macrophylla × *E. americana*	42×25-1	1	PT 820543	WA 75s1136 (F) WA 75c1171 (M)
E. macrophylla × *E. berteroana*	42×53-1	2	HO 82.280 PT 820253	PT 750420002 (F) PT 700044001 (M)
E. macrophylla × *E. berteroana*	42×53-2	2	HO 82.281	PT 700044001 (M)
E. macrophylla × *E. folkersii*	42×31-1	1	PT 820337	PT 750420002 (F) PT 700010001 (M)
E. macrophylla × *E. guatemalensis*	42×43-1	1	PT 820281	PT 750420002 (F) PT 700018001 (M)
E. macrophylla × *E. guatemalensis*	42×43-2	3	HO 82.763 PT 820544	WA 75s1136 (F) WA 74c1453 (M)

TABLE 11. *Continued.*

Hybrid	Hybrid Number	Live Plants	Hybrid Accession Numbers*	Parental Accession Numbers*
E. tajumulcensis × *E. guatemalensis*	40×43-1	4	HO 82.761 PT 820599	WA 74c1448 (F) WA 74c1453 (M)
	Sect. *Chirocalyx*			
E. abyssinica × *E. latissima*	95×94-1	1	HO 82.867	PT 770034001 (F) PT 750281004 (M)
	Sect. *Erythraster*			
E. perrieri × *E. variegata*	106×96-1	5	HO 82.768 PT 820550	WA 75s857 (F) WA 74s892 (M)
E. perrieri × *E. variegata*	106×96-2	3	HO 82.769 PT 820551	WA 74s892 (M) WA 74s892 (M)
E. perrieri × *E. variegata*	106×96-3	1	HO 82.770	WA 74s892 (M)

* HO = Ho'omaluhia Botanic Garden; PT = Pacific Tropical Botanical Garden; WA = Waimea Arboretum; F = female parent; M = male parent.

in growth rates, but they also produced flowers at an exceptionally early age. Many of the narrow hybrids between species in sect. *Erythrina* grew to be 4-m trees within two years after the seeds were sown, and most flowered within that time. Such sexual precocity is unknown in the parental species. Seeds from intraspecific matings were sown concurrently and in the same nursery with the hybrids; none grew as rapidly or flowered as early as most of the hybrids. None of the parental species, in cultivation, have been known to produce flowers in less than three years from seed.

An even more phenomenal case of precocious flowering was the intersectional (medium) hybrid *Erythrina crista-galli* × *E. fusca*. Two sibling individuals of this combination (PT 840231001 and -002) produced flowers when they were still small plants in nursery pots less than five months after the seeds were sown. The parentals are both large- to medium-sized trees and are not known to flower in the wild or in cultivation before at least several years of growth.

Twenty-five of the two-year-old F_1 hybrid plants flowered during February–March 1984. All were narrow hybrids within sect. *Erythrina*, and represented nine hybrid combinations. These are listed in Table 14 with the pollen fertility of each individual. Also included in Table 14 is the pollen fertility of each of the parental individuals from which these hybrids were derived.

With two exceptions, the pollen fertility of the F_1 hybrids was above 95%. The pollen fertility of the hybrids ($\bar{X} = 97.6\%$) was slightly but significantly higher ($P < 0.05$) than the fertility of the parentals ($\bar{X} = 95.0\%$). Eighteen of the 25 hybrid individuals had pollen fertilities higher than either of their parents. For this trait at least, the narrow hybrids in sect. *Erythrina* clearly exhibited interspecific heterosis.

Meiosis in pollen mother cells was examined in several of the F_1 hybrids in sect. *Erythrina*. An example is *Erythrina guatemalensis* × *E. macrophylla*, HO 82.288-A (Figs. 9, 10). Meiotic behavior in this hybrid can be compared with meiosis in its male parent *E. macrophylla*, PT 750420002 (Figs. 5, 6).

As in the parental species, meiosis in the hybrids was characterized by clumping of bivalents at late diakinesis and metaphase I and by "sticky" chromatin bridges and late disjunction of some bivalents at anaphase I. The normal meiotic process was, however, not disrupted. Nondisjunction or unequal assortment of chromosomes during meiosis I was not observed, and all cells examined at telophase I or subsequent stages had the expected number of 21 chromosomes. Meiotic behavior in the F_1 hybrids within sect. *Erythrina*, in short, was identical to the behavior described above for the parental species.

The only intersectional F_1 hybrid to flower by November 1984 was the five-month-old *Erythrina crista-galli* × *E. fusca*. Pollen fertility in this hybrid (PT 840231001) was 81%. This was lower than the pollen fertility of either parent (*E. crista-galli*, WA 74p840, 96.1%; *E. fusca*, WA 74s99, 96.3%) but probably not low enough to affect substantially fertility and mating success of the hybrid. Only limited material was available for analysis of meiosis in pollen mother cells of *E. crista-galli* × *E. fusca*. In some cells, several quadrivalents ap-

TABLE 12. *Artificial* Erythrina *hybrids: medium (between sections, within subgenera).*

Hybrid[1]	Hybrid Number	Live Plants	Hybrid Accession Numbers	Parental Accession Numbers
	Subg. *Duchassaingia*			
E. crista-galli (2) × *E. fusca* (1)	2×1-1	2	HO 84.234	PT 740283001 (F)
			PT 840232	PT 740230005 (M)
E. crista-galli (2) × *E. fusca* (1)	2×1-2	5	HO 84.235	WA 74p840 (F)
			PT 840231	WA 74s99 (M)
	Subg. *Erythrina*			
E. herbacea (12) × *E. humeana* (18)	22×73-1	2	HO 82.863	WA 76s187 (F)
			PT 820697	WA 74p1382 (M)
E. lysistemon (17) × *E. speciosa* (9)	72×16-1	1	HO 84.238	PT 750280003 (F)
				PT 730708001 (M)
E. lysistemon (17) × *E. speciosa* (9)	72×16-2	2	HO 84.243	PT 750280002 (F)
				PT 730708001 (M)
E. speciosa (9) × *E. lysistemon* (17)	16×72-1	1	HO 84.236	PT 730708003 (F)
				PT 750280003 (M)
E. speciosa (9) × *E. lysistemon* (17)	16×72-2	3	HO 84.237	PT 730742002 (F)
				PT 750280003 (M)

[1] Number in parentheses after each species denotes section (see Table 1).

peared to be formed at metaphase I (Fig. 11). In other cells, meiosis was normal with 21 bivalents at metaphase I. Without more thorough cytological analyses, it is not possible to state whether or not meiosis is significantly disrupted in this hybrid. Nondisjunction and unequal segregation of some chromosomes may contribute to the partial reduction in fertility of the pollen.

Fecundity of F_1 Hybrids. Fruit maturation from the controlled self-pollinations of the two-year-old F_1 hybrids in sect. *Erythrina* (Table 15) was very low, less than 3%, and nine of the 12 F_1s produced no fruits from controlled selfing. In common with the usual pattern of results in experimental pollinations of *Erythrina* parentals, much of the failure in fruit maturation was due to postzygotic abortion of young fruits, within one or two weeks after fertilization. Most of the F_1s did produce a few fruits spontaneously, on open-pollinated inflorescences. Animal pollen vectors were not present in the garden plots, and it is most likely that these open-pollinated fruits were produced by autogamy.

TABLE 13. *Artificial* Erythrina *hybrids: wide (intersubgeneric).*

Hybrid[1]	Hybrid Number	Live Plants	Hybrid Accession Numbers	Parental Accession Numbers
E. caffra (17) × *E. fusca* (1)	71×1-1	2	PT 820422	WA 74c1456 (F)
				WA 74s99 (M)
E. crista-galli (2) × *E. guatemalensis* (12)	2×43-3	8	HO 82.758	WA 74p840 (F)
			PT 820598	WA 74c1453 (M)
E. crista-galli (2) × *E. speciosa* (9)	2×16-1	1	HO 82.860	WA 740283001 (F)
				PT 730708001 (M)
E. crista-galli (2) × *E. variegata* (26)	2×96-2	1	HO 82.495	WA 74p840 (F)
				WA 76s996 (M)
E. guatemalensis (12) × *E. abyssinica* (25)	43×95-1	1	HO 84.287	PT 700018001 (F)
				PT 731006002 (M)
E. guatemalensis (12) × *E. senegalensis* (22)	43×79-2	1	HO 82.766	WA 74c1453 (F)
				WA 74s100 (M)
E. herbacea (12) × *E. fusca* (1)	22×1-1	4	HO 82.634	WA 75c1103 (F)
			PT 820542	WA 74s99 (M)

[1] Number in parentheses after each species denotes section (see Table 1).

TABLE 14. *Pollen fertility of artificial F_1 hybrids within sect.* Erythrina *and of their parents. At least 500 grains counted for all samples.*

I. Hybrids

Hybrid Combination	Accession Number	Percent Normal Grains
E. americana × *E. berteroana*	PT 820420001	99.4*
E. berteroana × *E. guatemalensis*	PT 820549001	96.7
E. berteroana × *E. guatemalensis*	HO 82.647-A	86.3
E. chiapasana × *E. berteroana*	HO 82.278-A	98.1
E. chiapasana × *E. berteroana*	HO 82.278-B	99.6*
E. chiapasana × *E. berteroana*	HO 82.278-C	99.6*
E. chiapasana × *E. berteroana*	HO 82.278-D	99.5*
E. guatemalensis × *E. berteroana*	PT 820493001	97.3*
E. guatemalensis × *E. berteroana*	PT 820493002	96.3
E. guatemalensis × *E. chiapasana*	HO 82.283-A	99.8*
E. guatemalensis × *E. chiapasana*	PT 820254002	96.6
E. guatemalensis × *E. chiapasana*	HO 82.284-A	98.6*
E. guatemalensis × *E. chiapasana*	HO 82.284-B	98.8*
E. guatemalensis × *E. chiapasana*	HO 82.284-E	99.1*
E. guatemalensis × *E. folkersii*	HO 82.282-A	99.4*
E. guatemalensis × *E. folkersii*	HO 82.282-B	98.4*
E. guatemalensis × *E. macrophylla*	HO 82.285-B	99.6*
E. guatemalensis × *E. macrophylla*	HO 82.288-A	97.8*
E. guatemalensis × *E. macrophylla*	PT 820276001	98.2*
E. guatemalensis × *E. standleyana*	HO 82.765-A	89.8
E. guatemalensis × *E. tajumulcensis*	PT 820547001	99.4*
E. macrophylla × *E. berteroana*	HO 82.281-A	98.8*
E. macrophylla × *E. berteroana*	HO 82.281-B	98.2*
E. macrophylla × *E. guatemalensis*	HO 82.763-A	96.4
E. macrophylla × *E. guatemalensis*	HO 82.763-B	98.6*

TABLE 14. *Continued.*

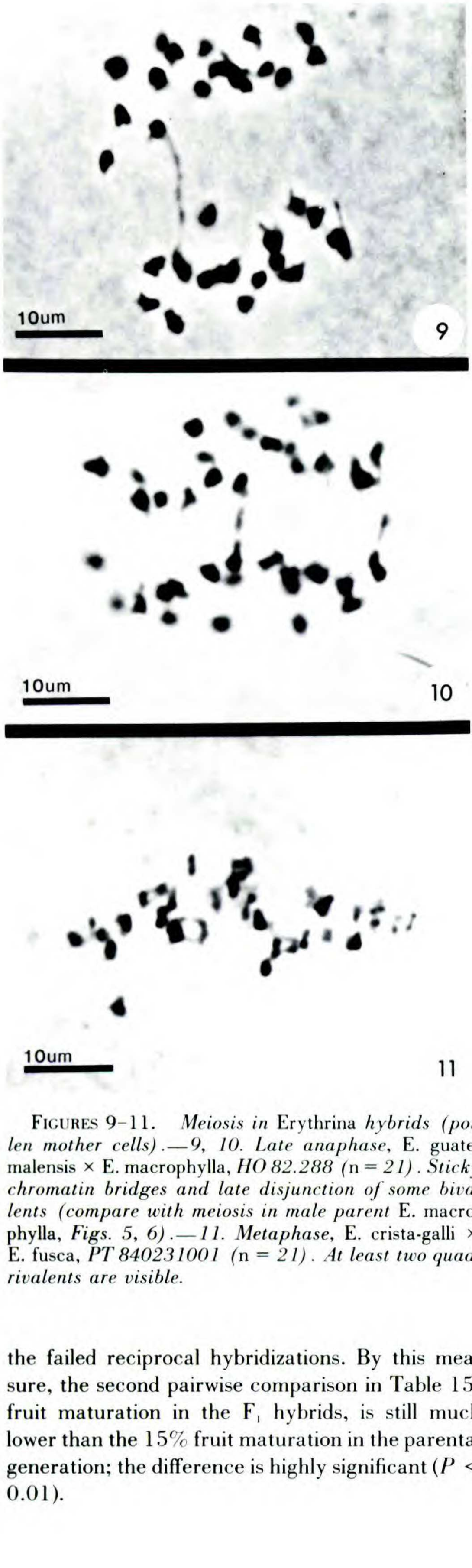
II. Parentals

Species	Accession Number	Percent Normal Grains
E. americana	WA 75c1171	97.3
E. berteroana	WA 74s864	96.6
E. berteroana	WA 78s564	97.2
E. berteroana	PT 700044001	96.4
E. berteroana	PT 700044002	98.1
E. berteroana	PT 730711001	97.4
E. chiapasana	PT 730710001	96.3
E. chiapasana	PT 721005001	94.4
E. folkersii	PT 700010001	85.3
E. guatemalensis	PT 70018001	97.7
E. guatemalensis	WA 74c1453	97.7
E. guatemalensis	PT 750419001	91.4
E. macrophylla	PT 750420002	94.4
E. macrophylla	WA 75s1136	96.9
E. standleyana	WA 75s1056	84.9
E. tajumulcensis	WA 74c1448	98.0

Hybrids: mean pollen fertility = 97.6% ± 3.0%.
Parentals: mean pollen fertility = 95.0% ± 4.1%.
Differences in pollen fertility, hybrids vs. parentals: $t = 2.28$; DF = 39; $P < 0.05$.
* Indicates hybrids with higher pollen fertility than either parent.

Also in Table 15 are comparisons of fruit maturation in the selfed F_1 hybrids vs. their parents. Several combinations of parental matings are included in the analyses. Fruit maturation was much lower in the selfed F_1s (3%) than in the original hybridizations which produced these F_1s (22%) ($P < 0.01$).

The second pairwise comparison of fruit maturation in Table 15, selfed F_1 hybrids vs. all of their parental hybrid combinations (including reciprocals), may be more biologically meaningful than the first comparison for the following reason: the female parents of the F_1 hybrids were very fecund, with higher than average fruit maturation. The male parents (pollen donors) of the F_1s generally had lower fruit maturation when employed as females in the hybridization trials; many of the reciprocal crosses produced no hybrid fruit at all. If it is assumed that fecundity (fruit maturation) is a quantitatively heritable trait, then an F_1 hybrid might be expected to be intermediate in fecundity between its two parents, providing there is no reduction in fruit maturation in the hybrid caused by incompatibilities between its constituent genomes. The proportion of fruit maturation expected in the F_1s, then, should approximate the proportion in all the parental hybrid combinations, including



FIGURES 9–11. *Meiosis in* Erythrina *hybrids (pollen mother cells).—9, 10. Late anaphase,* E. guatemalensis × E. macrophylla, *HO 82.288* (n = *21*). *Sticky chromatin bridges and late disjunction of some bivalents (compare with meiosis in male parent* E. macrophylla, *Figs. 5, 6).—11. Metaphase,* E. crista-galli × E. fusca, *PT 840231001* (n = *21*). *At least two quadrivalents are visible.*

the failed reciprocal hybridizations. By this measure, the second pairwise comparison in Table 15, fruit maturation in the F_1 hybrids, is still much lower than the 15% fruit maturation in the parental generation; the difference is highly significant ($P < 0.01$).

There are several possible reasons for the reduced fruit maturation in the F_1 hybrids in sect. *Erythrina*. The first is that the low fecundity is in fact a consequence of hybridity caused by genic incompatibility between the parental genomes. It is evidently not, however, a matter of "hybrid sterility" in the usual sense of the term, in which the microgametophytes (pollen) and/or megagametophytes (embryo sacs) borne on the F_1 sporophyte are abortive and nonfunctional (Grant, 1953; Stebbins, 1958). The pollen fertility of the F_1 hybrids, as discussed above, was exceptionally high; the pistil and ovules also appeared to develop normally in the hybrids. Much of the failure of fruit set in the selfed F_1s was at the postzygotic stage (abortion of young fruits). If the reduced fecundity was truly a consequence of hybridity and intergenomic incompatibility, it is probably best considered as a case of "hybrid breakdown" (Grant, 1953; Stebbins, 1958) expressed as low viability of the F_2 embryos.

There are other possible explanations for the low fecundity of the selfed F_1s that do not invoke hybrid breakdown or other effects of hybridity. The first is that it may be a consequence of self-mating, the opposite effect from the apparent heterosis evidenced by the exceptional vigor of the F_1 plants. Fruit set in the selfed F_1s was significantly lower than the one in the selfed parentals, which in turn were significantly lower in fruit set than the hybridizations. For both parental and F_1 selfings, the high incidence of fruit abortion may be an expression of inbreeding depression, a result of the homozygous pairing of deleterious recessive alleles in the genomes of the embryos. This possibility could be tested by controlled cross-pollinations between F_1s, a step that was not taken initially because the goal of the F_1 selfings was to produce F_2 plants with no more than two constituent genomes.

Another possible reason for the low fecundity in the F_1s may simply be the juvenility of the F_1 plants themselves. Although the F_1s were very vigorous and flowered precociously at two years of age, they were not yet full-sized trees. At their size, they might not be able to draw on sufficient resources for the full fruit crop of a larger adult.

In short, the variables accounting for reduced fecundity in the narrow F_1 hybrids still need to be sorted out. This should be possible once the F_1 trees attain their full adult size and several categories of matings within and between individuals are carried out.

Viability of F_2 Hybrids. The viability of the F_2 hybrid seed, obtained from selfed and open-pollinated F_1 plants in sect. *Erythrina* (Table 16), was

TABLE 15. *Fruit and seed maturation from controlled self-pollinations of narrow F_1 hybrids in sect.* Erythrina.

Hybrid Combination	Accession Number	Flowers Pollinated	Mature Fruits	Total Number of Seeds
E. berteroana × *E. guatemalensis*	HO 82.674-A	18	0	0
E. guatemalensis × *E. berteroana*	PT 820493002	13	0	0
E. guatemalensis × *E. chiapasana*	HO 82.284-A	32	3	7
E. guatemalensis × *E. chiapasana*	HO 82.284-B	6	0	0
E. guatemalensis × *E. chiapasana*	HO 82.283-A	38	0	0
E. guatemalensis × *E. chiapasana*	PT 820254002	7	2	3
E. guatemalensis × *E. chiapasana*	PT 820278002	10	0	0
E. guatemalensis × *E. macrophylla*	HO 82.288-A	27	0	0
E. guatemalensis × *E. macrophylla*	HO 82.285-B	16	0	0
E. guatemalensis × *E. tajumulcensis*	HO 820547001	20	1	1
E. macrophylla × *E. berteroana*	HO 82.281-B	23	0	0
E. macrophylla × *E. guatemalensis*	HO 82.763-A	15	0	0
Total selfed F_1 hybrids		225	6 (3%)	11
Parental hybridizations		51	21 (22%)	
All parental hybrid combinations (including reciprocals)		171	25 (15%)	
Selfed parentals (sect. *Erythrina*)		144	12 (8%)	

Multiple comparison test for differences in fruit maturation

Selfed F_1s vs. parental hybridizations	$P < 0.01$
Selfed F_1s vs. all parental hybrid combinations	$P < 0.01$
Selfed F_1s vs. selfed parentals	$P < 0.05$
Parental hybridizations vs. selfed parentals	$P < 0.01$
All parental hybrid combinations vs. selfed parentals	N.S.

significantly lower than viability of the F_1 hybrids. This was shown in Table 8, where the F_2s were compared with all the narrow F_1 hybrids; the difference was highly significant ($P < 0.01$). In Table 16 the viability of the F_2 seed is compared specifically with that of their own parents, i.e., with the F_1 seed lots producing the parents of the F_2s. The viability of the F_2s (13%) was significantly lower ($P < 0.01$) than that of their F_1 parent generation (61% viability).

In Table 16 the viability of the F_2 seed and of their F_1 parents is also compared with seed from intraspecific matings in *Erythrina guatemalensis* (including seed from selfings and intraspecific outcrosses, the only intraspecific viability data available for sect. *Erythrina*). The F_1 hybrid seed was significantly higher in viability than the intraspecific seed ($P < 0.05$). The viability of the intraspecific seed (19%) was somewhat higher than that of the F_2 seed, but the difference was nonsignificant.

In summary, the viability of F_1 hybrid seed was significantly higher than F_2 seed derived from selfed F_1 matings and higher than seed derived from intraspecific matings. If the very high F_1 viability is truly an expression of interspecific heterosis, this hybrid advantage is not retained in the F_2 generation, when the F_2s are derived from selfed F_1 hybrids.

It is possible to interpret the reduction in F_2 viability with respect to F_1 viability as "hybrid breakdown." However, with the data presently available, the reduced viability of the F_2s derived from selfed F_1s could also be interpreted as an expression of inbreeding depression. It could also be interpreted simply as an absence of the heterotic advantage possessed by the F_1s, since the viability of the F_2s was not significantly lower than that of the intraspecific progeny. These three alternatives cannot be differentiated with the presently available information. Additional progeny trials of F_1, F_2, and intraspecific seed lots are needed to test the possibility that hybrid breakdown may be expressed in the F_2 generation of *Erythrina* hybrids.

In any case, the lowered average viability of the F_2s was a function only of poor germination of the seed. The seeds that did germinate produced healthy plants with normal growth and vigor at six months of age. There were no indications of chlorosis or other debilities in the F_2 plants.

Studies of Previously Synthesized Hybrids. Nine artificially produced *Erythrina* hybrids, all between

TABLE 16. *Viability of F_2 hybrids within sect.* Erythrina.

F_2 Hybrid Combination	Accession Number	Female Parent (F_1 Hybrid)	Paternity	Seeds Sown	Live F_2 Plants
E. guatemalensis × *E. berteroana*	HO 84.288	HO 82.641-A	Open	9	0
E. guatemalensis × *E. chiapasana*	PT 840234 PT 840235	PT 820254002	Self	3	0
E. guatemalensis × *E. chiapasana*	HO 84.289	HO 82.284-A	Self	7	1
E. guatemalensis × *E. macrophylla*	HO 84.290	HO 82.288-A	Open	5	1
E. guatemalensis × *E. tajumulcensis*	PT 840243	PT 820547001	Self	1	0
E. herbacea × *E. guatemalensis*	PT 840241	PT 820421001	Open	5	0
E. macrophylla × *E. berteroana*	HO 84.245	HO 82.281-A	Open	4	1
E. macrophylla × *E. berteroana*	HO 84.291	HO 82.281-B	Open	4	4
E. macrophylla × *E. guatemalensis*	HO 84.244 HO 84.292 PT 840242	HO 82.763-B	Open	18	1
Total F_2 hybrids in sect. *Erythrina*				56	7 (13%)
F_1 hybrid parents of F_2s				28	17 (61%)
Intraspecific progeny, *Erythrina guatemalensis*				26	5 (19%)

Multiple comparison test for differences in viability of seed

F_2 hybrids vs. their F_1 hybrid parents	$P < 0.01$
F_2 hybrids vs. intraspecific *E. guatemalensis*	N.S.
F_1 hybrids vs. intraspecific *E. guatemalensis*	$P < 0.01$

species of different sections, have been reported prior to this study (Table 17). Krukoff & Barneby (1974) described most of these; in the same paper they described some putative natural hybrids between sympatric Mesoamerican and African species. The parentage of only two of the artificial hybrids is known for certain; both of these F_1s are "wide" intersubgeneric hybrids and are reported to be fertile.

The oldest and best-known *Erythrina* hybrid is *E.* ×*bidwillii* Lindley, synthesized from *E. herbacea* (sect. *Erythrina*) ♀ and *E. crista-galli* (sect. *Cristae-galli*) ♂ in Australia in the 1840s and since spread around the world as a cultivar by propagation of cuttings. Krukoff & Barneby (1974) reported *E.* ×*bidwillii* to produce viable seed and also that "no Mendelian segregation of phenetic characters is observed in the F_1 or subsequent generations." They further claimed that this hybrid had naturalized in Fiji and was therefore a stabilized "neospecies."

I examined *E.* ×*bidwillii* in cultivation at Foster Garden, Honolulu (FG 64.2035). Meiosis in pollen mother cells was normal with 21 bivalents at metaphase I. Pollen fertility was 63%, comparable to Graham & Tomb's (1974) report of 76% normal pollen for this hybrid. I attempted to produce an F_2 generation by controlled self-pollination of 60 flowers over a period of several weeks. Young fruits were obtained but they invariably aborted before two weeks of development. I have not seen mature spontaneously produced fruits on any cultivated plants or herbarium specimens of *E.* ×*bidwillii*, so the reports of its viable seed production are questionable.

I made limited attempts (12 trial pollinations) to backcross *E.* ×*bidwillii* to one of its parents, *E. crista-galli*. The pollinations all failed, but given the reasonably high pollen fertility of *E.* ×*bidwillii*, it is likely that with perseverance some backcross progeny could be obtained.

The other previously reported hybrid of known parentage is *Erythrina* ×*resuparcellii* Srivastava (a *nomen nudum*, not validly published), a hybrid between the perennial herb *E. resupinata* (sect. *Suberosae*) ♀ and *E. variegata* (sect. *Erythraster*) ♂ (Jalil et al., 1982). The F_1 is a branched shrub, and in other morphological traits is also intermediate between the two parents. The flowers, however, resemble those of the female parent much more closely than those of the male. This hybrid was not available to me, but Jalil et al. (1982) reported that it had normal meiosis in pollen mother cells with 21_{II} at metaphase I, pollen fertility of 62%, and viable seed.

Erythrina ×*sykesii* Barneby & Krukoff was the only other hybrid among those listed in Table 17 available to me for experimental studies. This

TABLE 17. *Previous reports of artificial* Erythrina *hybrids.*[1]

1. *Erythrina* ×*bidwillii* Lindley, Bot. Reg. 33: pl. 9. 1849.
   E. herbacea ♀ (12) × *E. crista-galli* ♂ (2)
2. *Erythrina* ×*bellangeri* Focke, Die Pflanzen-mischlinge. 110. 1881.
   ? *E. crista-galli* ♀ (2) × *E. herbacea* ♂ (12)
3. *Erythrina* ×*crassifolia* Koorders ex Backer, Schoolflora voor Java 1: 360. 1911.
   ? *E. subumbrans* (6) × *E. variegata* (26)
   ? *E. fusca* (1) × *E. variegata* (26)
4. *Erythrina* ×*fluminensis* Barneby & Krukoff, Lloydia 37: 446. 1974.
   ? *E. speciosa* (9) × *E.* sp. (subg. *Micropteryx*)
5. *Erythrina* ×*hennesyae* Barneby & Krukoff, Lloydia 37: 448. 1974.
   ? *E. humeana* (18) × *E. lysistemon* (17)
6. *Erythrina* ×*orba* Barneby & Krukoff, Lloydia 37: 449. 1974.
   E. lysistemon (17) × *E. speciosa* (9)
7. *Erythrina* ×*sykesii* Barneby & Krukoff, Lloydia 37: 447. 1974.
   ? *E. americana* (12) × *E. lysistemon* (17)
   ? *E. speciosa* (9) × *E. lysistemon* (17)
8. *Erythrina* ×*vlissingensis* Waby ex Barneby & Krukoff, Lloydia 37: 446. 1974.
   ? *E. fusca* (1) × *E. variegata* (26)
   ? *E. fusca* (1) × *E. suberosa* (4)
9. *Erythrina* ×*resuparcellii* Srivastava, Allertonia 3: 19. 1982. *nomen nudum.*
   E. resupinata ♀ (4) × *E. variegata* ♂ (26)

[1] Known or presumed parental species combinations are listed below each hybrid binomial; question mark preceding hybrid combination indicates uncertain parentage. Numbers in parentheses following species refer to sections to which species belong (Table 1).

hybrid was reputedly produced under cultivation in Australia in the 19th century, but its parentage is unknown. Krukoff & Barneby (1974) believed the parents to be *E. lysistemon* (sect. *Caffrae*) and *E. americana* (syn. *E. coralloides*) (sect. *Erythrina*). Based on study of floral and leaf morphology, I believe instead that the parents are *E. lysistemon* and *E. speciosa* (sect. *Stenotropis*). Since I have obtained both reciprocal hybrids of *E. speciosa* × *E. lysistemon* (Table 12), these F_1s can be compared with *E.* ×*sykesii* when they come into flower.

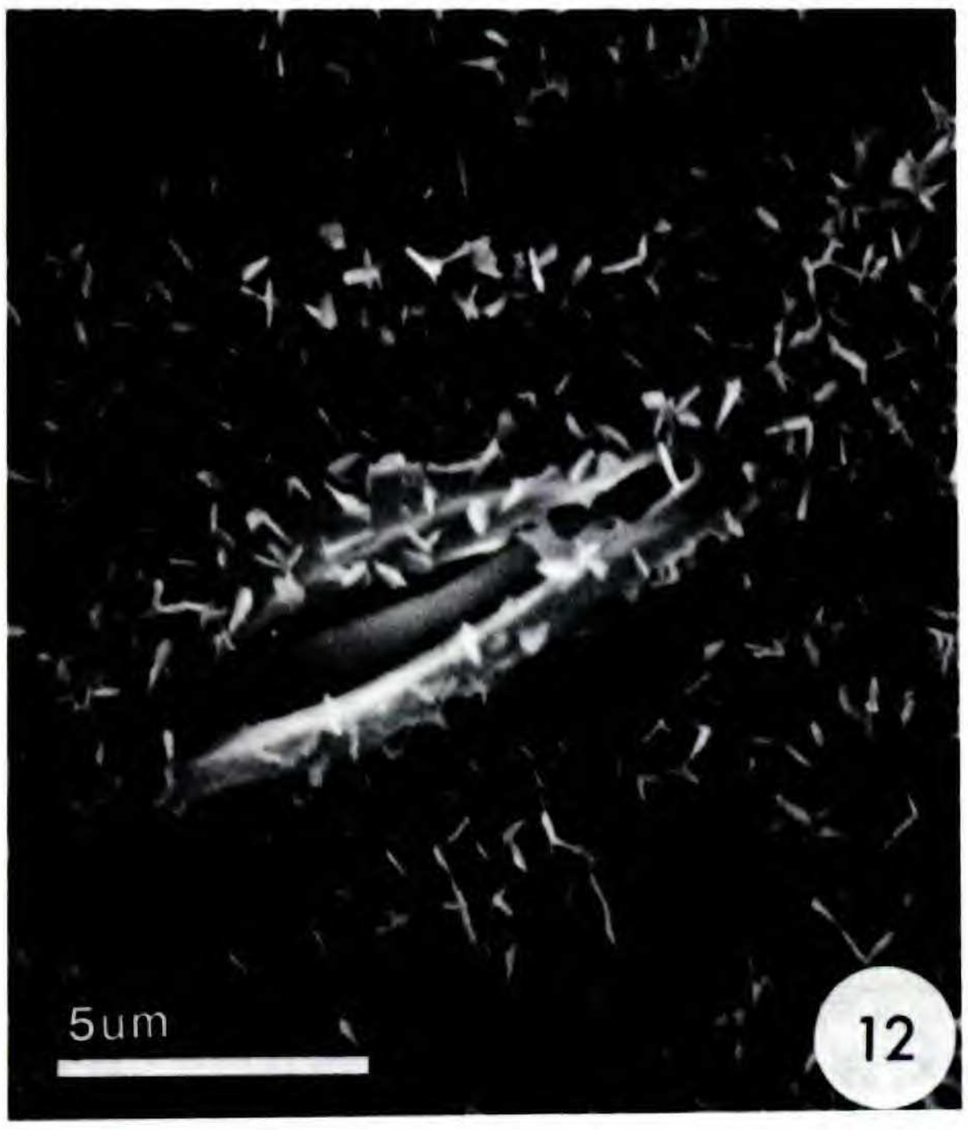
I examined cytologically several individual ramets of *E.* ×*sykesii* (WA 76p864, WA 75s1706, Foster Garden FL.669) and attempted to produce F_2 plants by controlled self-pollination. Meiosis in PMCs was apparently normal, with 21 bivalents at metaphase I. Pollen fertility was 81–84%, which agreed closely with results reported earlier for the same taxon by Graham & Tomb (1974). However, no mature fruits were obtained from 65 attempts at selfing. Young fruits with partially developed seeds were produced in abundance as with *E.* ×*bidwillii*, but these always aborted within two to three weeks following pollination.

Erythrina ×*bidwillii*, *E.* ×*resuparcellii*, and *E.* ×*sykesii* are the only intersectional or intersubgeneric hybrids that have been tested for fecundity at this time. An F_2 generation was reportedly obtained from *E.* ×*resuparcellii* (Jalil et al., 1982), but the other two may be incapable of producing F_2 progeny, at least from selfing of the F_1. Zygotes, embryos, and young fruits are formed, but the fruits abort before maturity. These "wide" hybrids, then, may be subject to hybrid breakdown expressed as inviability of the F_2 hybrid embryos borne on the F_1 hybrid sporophyte. As discussed in the previous section, the cause of mating failure in the F_1 hybrids is subject to different interpretations. Whether or not F_2 hybrid breakdown is a general phenomenon in *Erythrina* remains to be investigated.

CONCLUSIONS: EXPERIMENTAL HYBRIDIZATIONS AND SELF-COMPATIBILITY TRIALS

From the information presented in this section, a series of generalizations regarding breeding systems and species relationships in *Erythrina* can be outlined:

1. Even under the most carefully controlled conditions, mating success (proportion of pollinated flowers producing mature fruits) is low in all *Erythrina* species. This is true even when the effects of "resource competition" are eliminated by removing most flowers from an inflorescence as well as all of the spontaneously produced fruits on the tree, and pollinating only a few selected flowers per inflorescence. Mating failure results partly from prefertilization abortion of pollinated flowers, but also to a large extent from postfertilization abortion of young fruits.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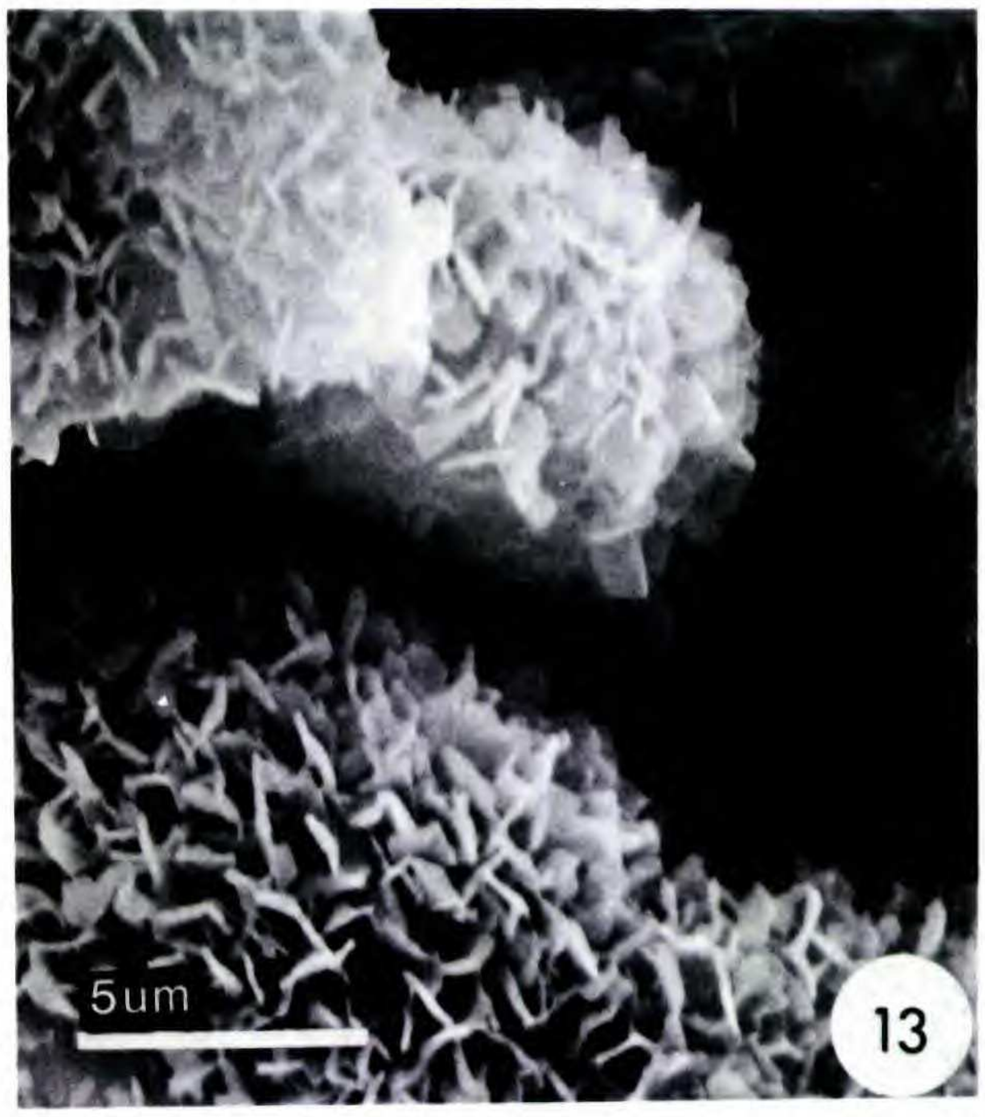
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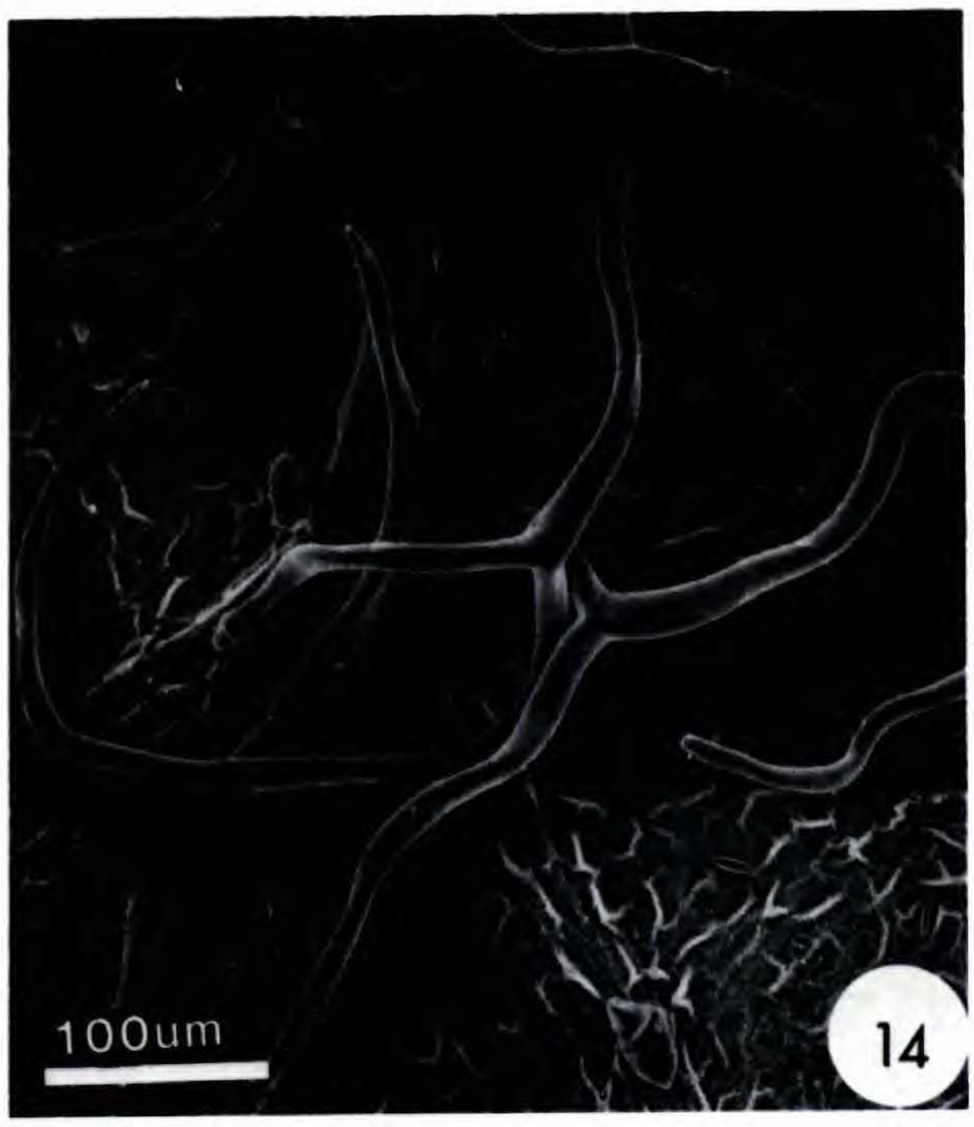
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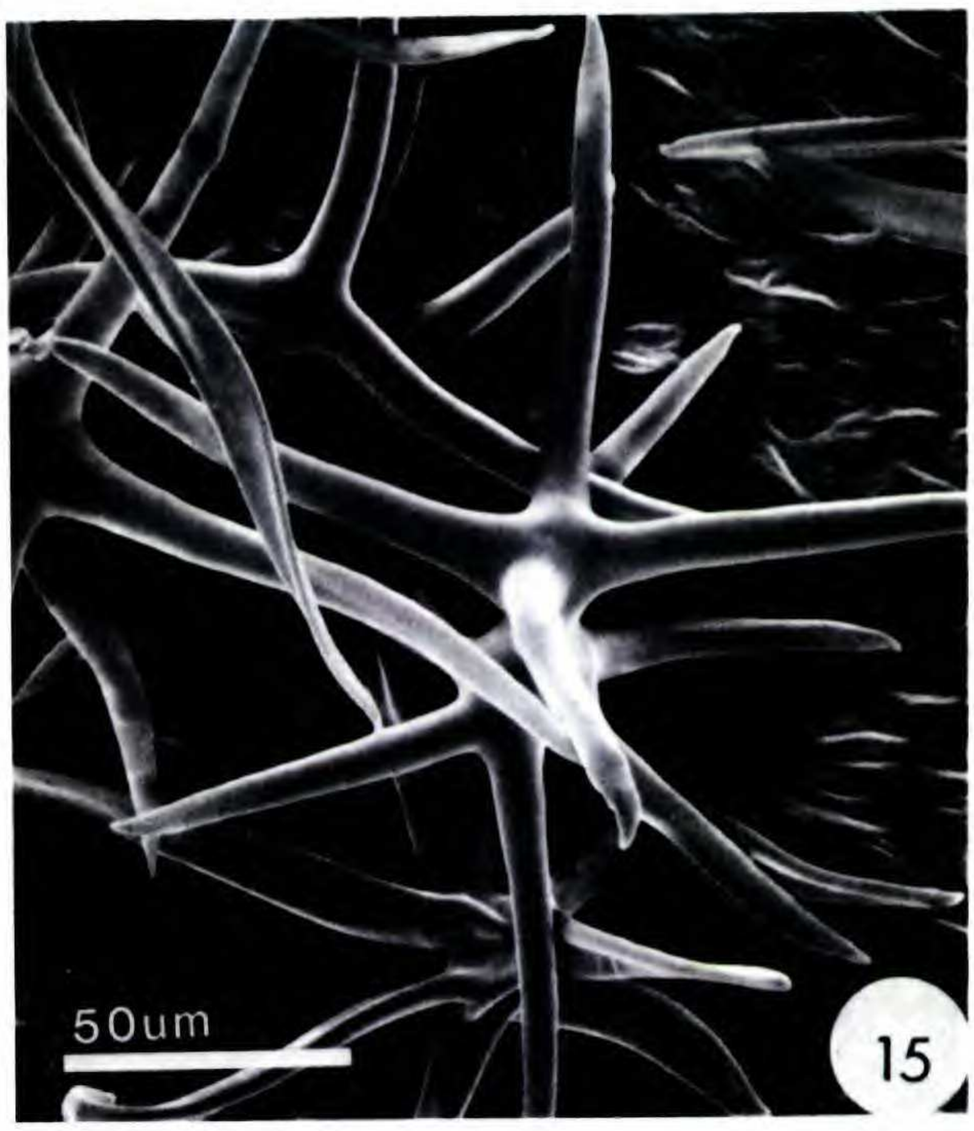
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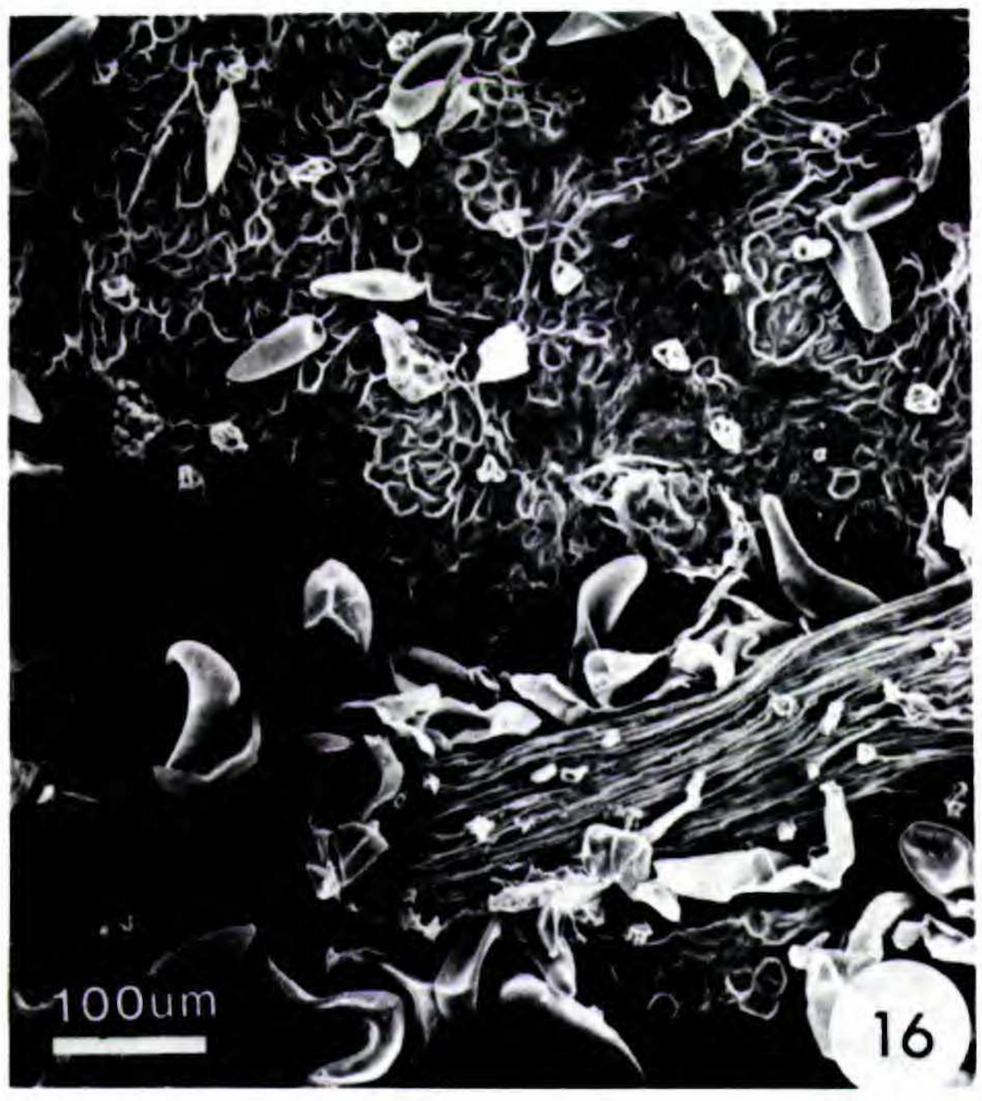
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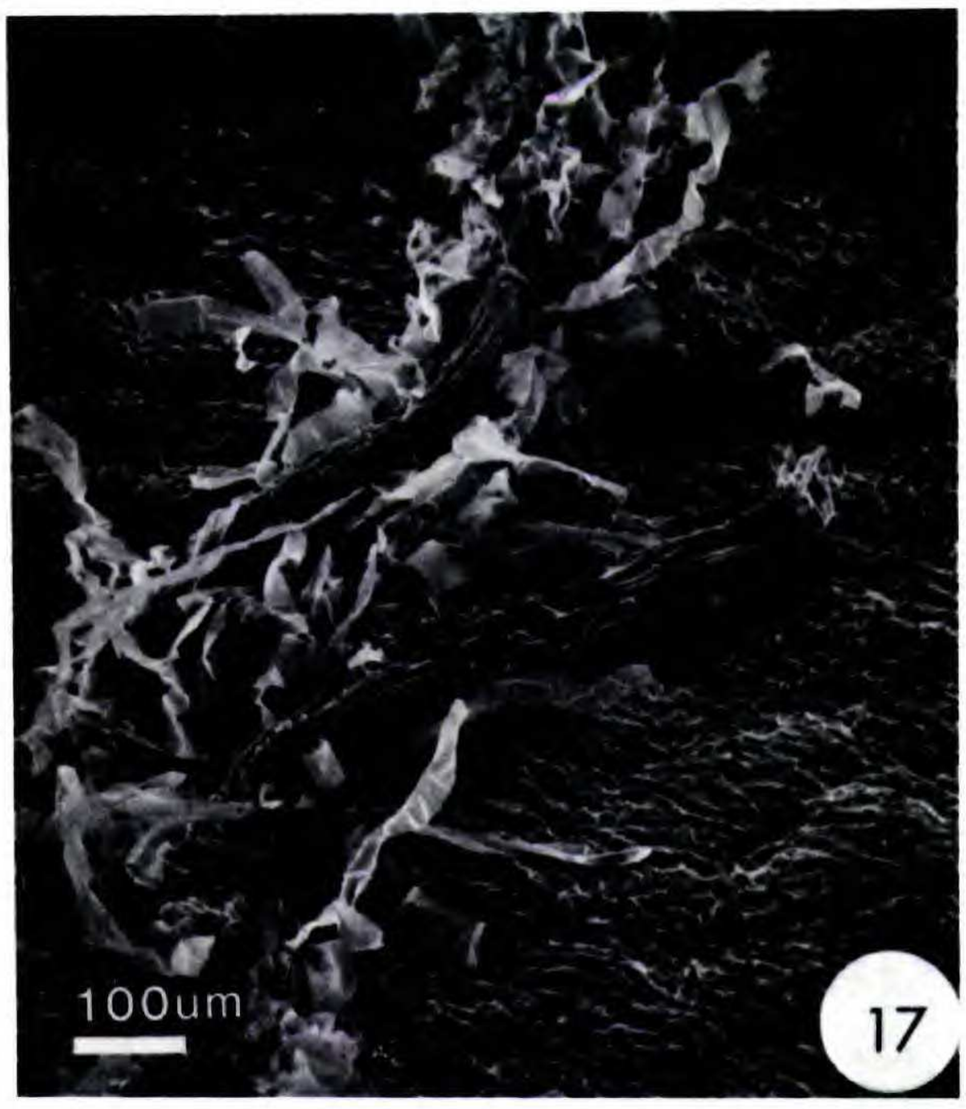
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2. Gametophytic or sporophytic self-incompatibility systems of the "classical" model, mediated by inhibition of pollen tubes in the style or stigma and governed by a single-locus, multiallelic S-gene, are evidently not present in any of the *Erythrina* species examined. Self-incompatibility in this strict sense is probably absent from the entire genus. There is considerable individual variation in fecundity, and some individuals may be cryptically female-sterile, but if an individual produces seed from outcrossing it will also produce some seed from self-mating. For some individuals and some populations, mating success is lower in selfing than in outcrosses, but much of the mating failure is expressed postzygotically by abortion of young fruits. This is probably an expression of inbreeding depression, the consequence of increased homozygosity for any number of deleterious recessive alleles, rather than the action of a specific S-allele. Inbreeding depression may also be expressed in the progamic stage as inhibition of pollen tubes.

3. Spatial separation of anthers and stigma in some *Erythrina* species, and protandry in other species, limits autogamous pollinations. For the protandrous species at least, this mechanism is not absolutely effective; autogamous fruits are occasionally produced. Autogamy occurs only with the ultimate flowers on an inflorescence and may be an adaptive feature of the breeding system to produce some seed as a "last resort" if no "high-quality" (i.e., outbred) seed was produced on earlier flowers of the inflorescence.

4. The hybridization trials indicate that matings between closely related species (within sections) are just as likely to produce viable progeny as are matings within species. Mating success is usually higher, in fact, in interspecific hybridizations within sections than in self-mating. At increasing taxonomic distance between parental species, there is a general trend to lower mating success in the hybridization trials. This trend is not universally applicable, however. Viable F_1 hybrids have been produced between the most distantly related groups of species in the genus—between species of different subgenera indigenous to different continents. It is probable that viable F_1 hybrids can be obtained between any two diploid species in the genus *Erythrina*.

5. F_1 hybrids between the closely related species in sect. *Erythrina* exhibit interspecific heterosis by several measures: viability of the F_1 seed is higher, and the F_1 plants are more vigorous, sexually precocious, and have higher pollen fertility than the parental species. Pollen fertility is somewhat lower in hybrids between more distantly related species, but these hybrids are generally comparable in viability and vigor with the parental species.

6. A reduction in fecundity is exhibited by the F_1 hybrids, at least when the F_1s are selfed. This lowered mating success is not due to "hybrid sterility" per se, since the gametes produced by the F_1 hybrid function normally. Mating failure is expressed postzygotically by abortion of young fruits and evidently is a consequence of inviability of the F_2 hybrid embryo. An alternative explanation may be that mating failure in the selfed F_1s is a consequence of inbreeding depression.

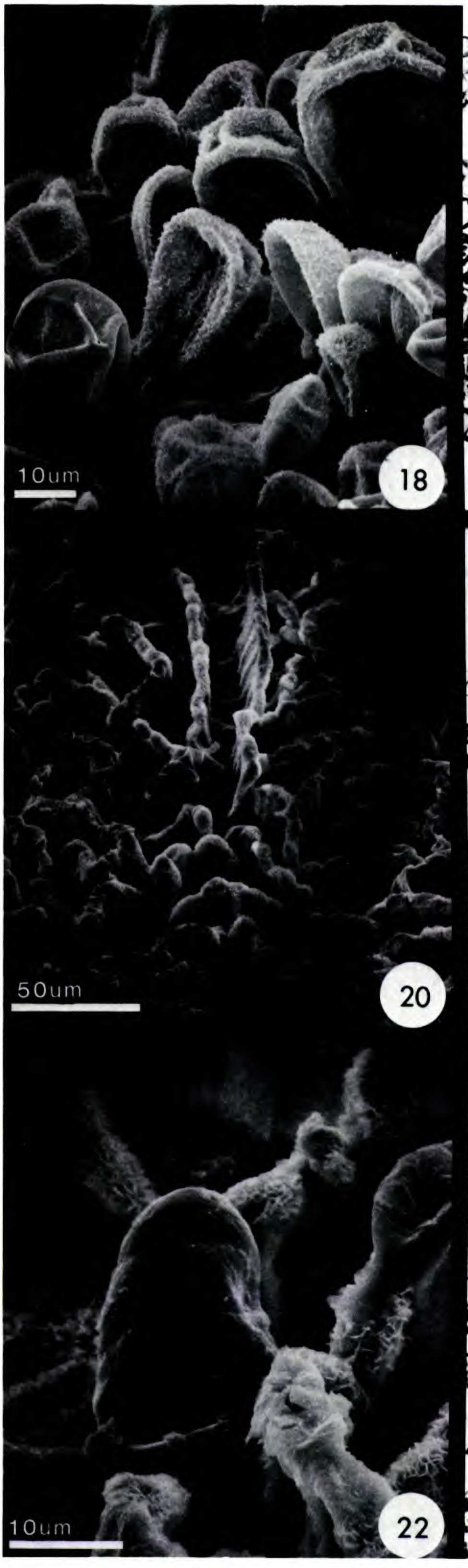
These experiments support the first two hypotheses presented in the introduction: 1) the species in sect. *Erythrina* can hybridize freely with each other, and there are no internal qualitative or quanitative postmating isolating barriers between the species; and 2) hybridization between more widely divergent species is also possible; there is generally a quantitative reduction in mating success in the wider hybridizations, but this probably does not constitute an absolute barrier to the formation of F_1 hybrids. The only major unanswered question regarding interspecific compatibility among diploid *Erythrina* is the possibility of hybrid breakdown in the F_2 and subsequent generations. F_2 breakdown, if it exists, does not form an absolute isolating barrier within sect. *Erythrina*, but it may form an absolute barrier in hybridizations between more widely divergent species.

Section 5. Inheritance of Phenetic Traits in Interspecific Hybrids

The fact that plant species with large morphological discontinuities can be hybridized, and that large hybrid progenies can be grown together in a common garden, has allowed for analyses of the genetic basis of these phenetic differences (review in Gottlieb, 1984). A thorough genetic analysis, of course, requires at least the study of segregating

←

Figures 12–17. *SEM images of abaxial leaf surface of* Erythrina.—*12. Epicuticular wax platelets*, E. suberosa, *WA 45s960.*—*13. Epicuticular wax platelets*, E. berteroana, *PT 700044001.*—*14. Two-armed hairs*, E. chiapasana, *WA 74s876.*—*15. Dendritic hairs*, E. perrieri, *WA 74s876.*—*16. Balloonlike hairs*, E. arborescens, *WA 78s225.*—*17. Ribbonlike hairs*, E. leptorhiza, Neill 5646.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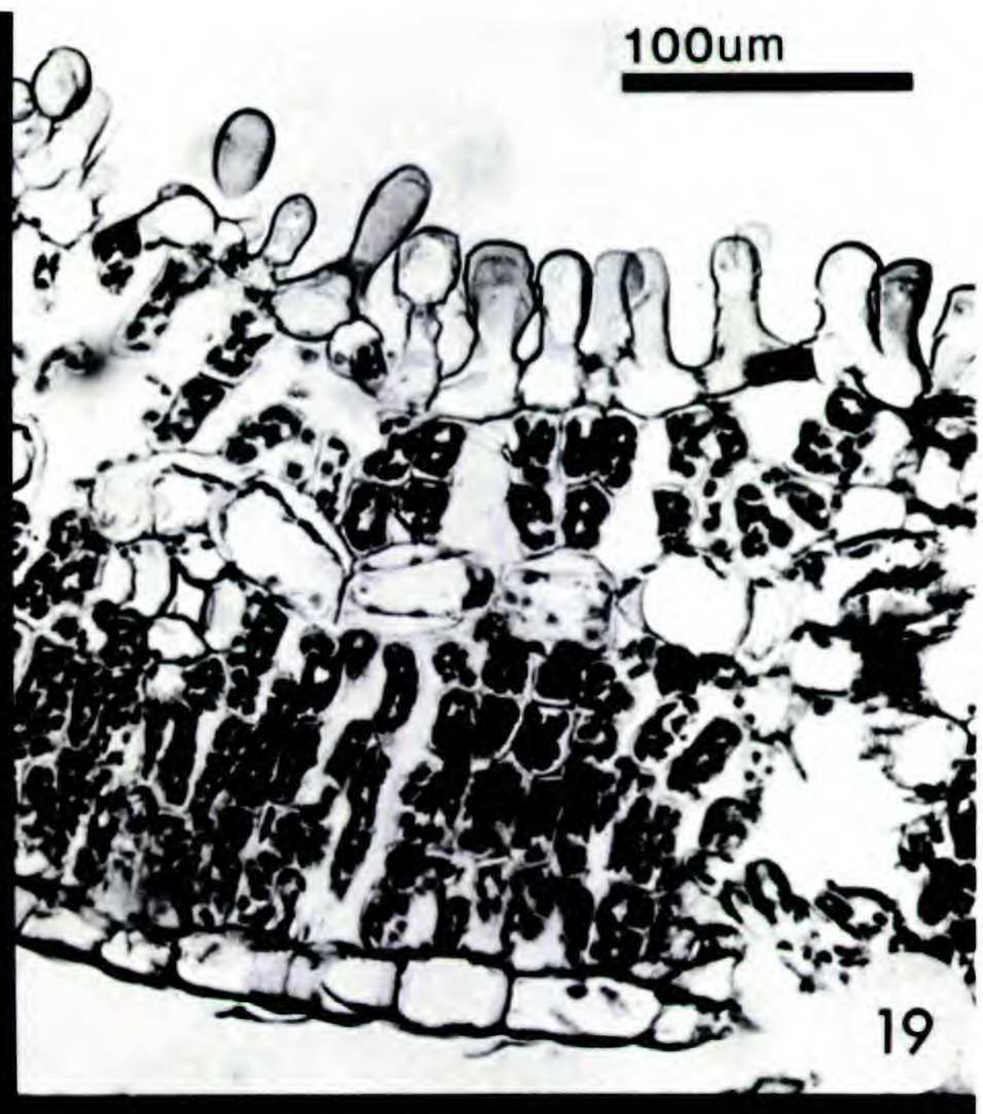
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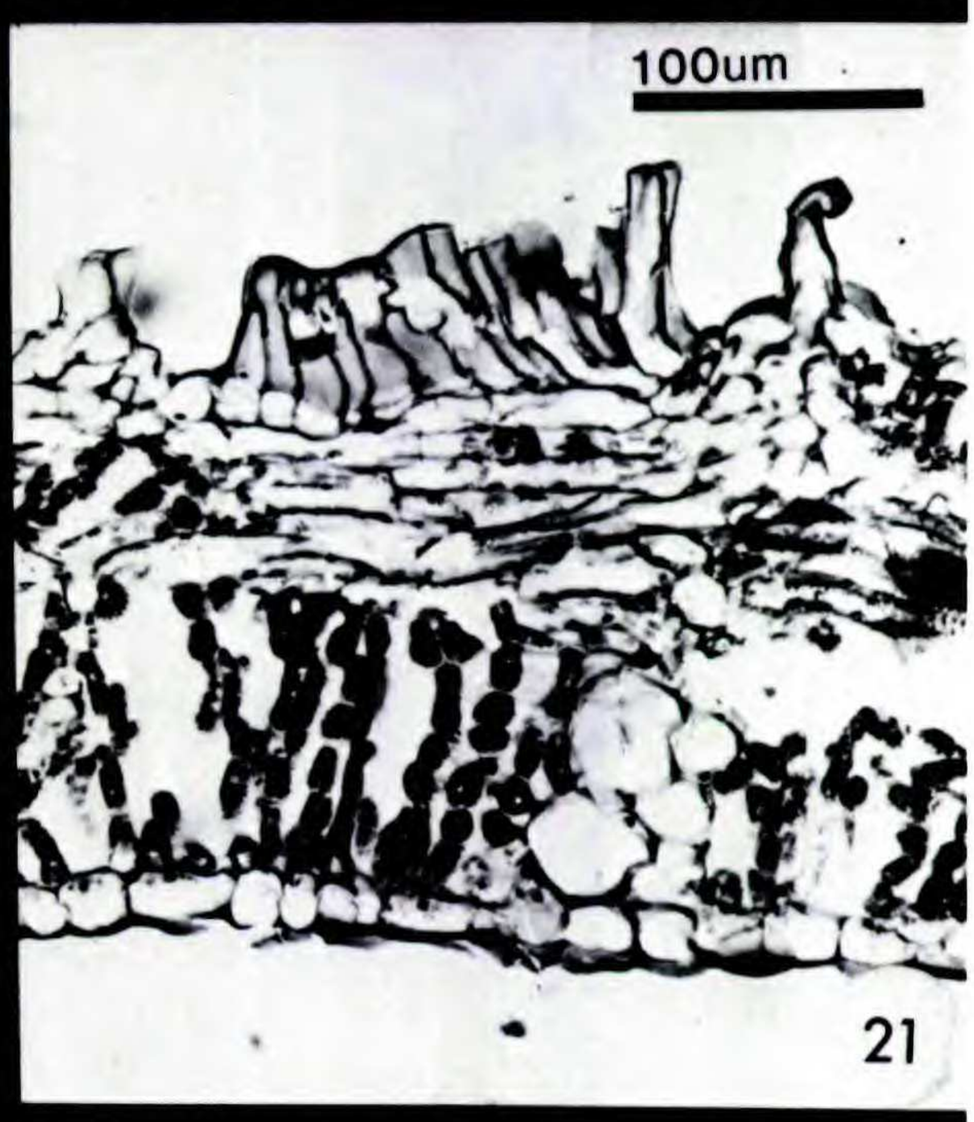
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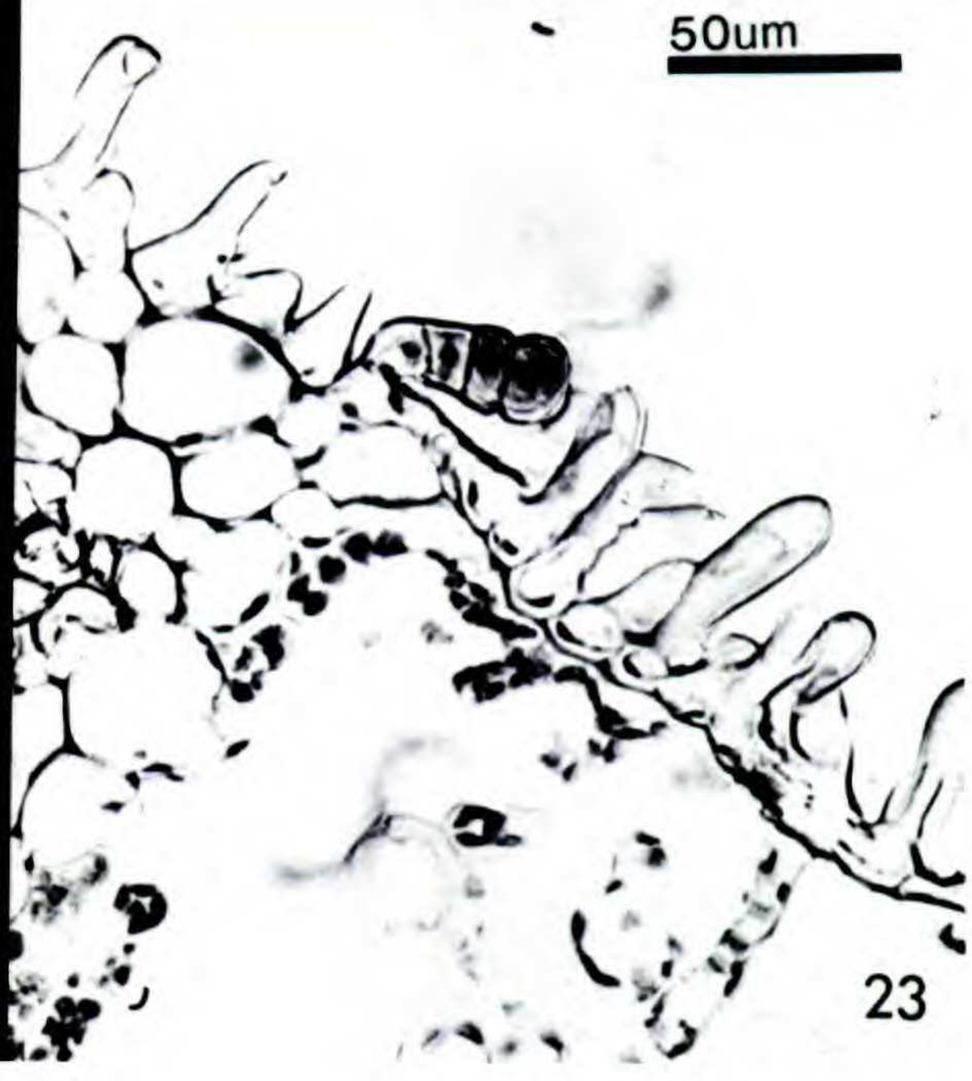
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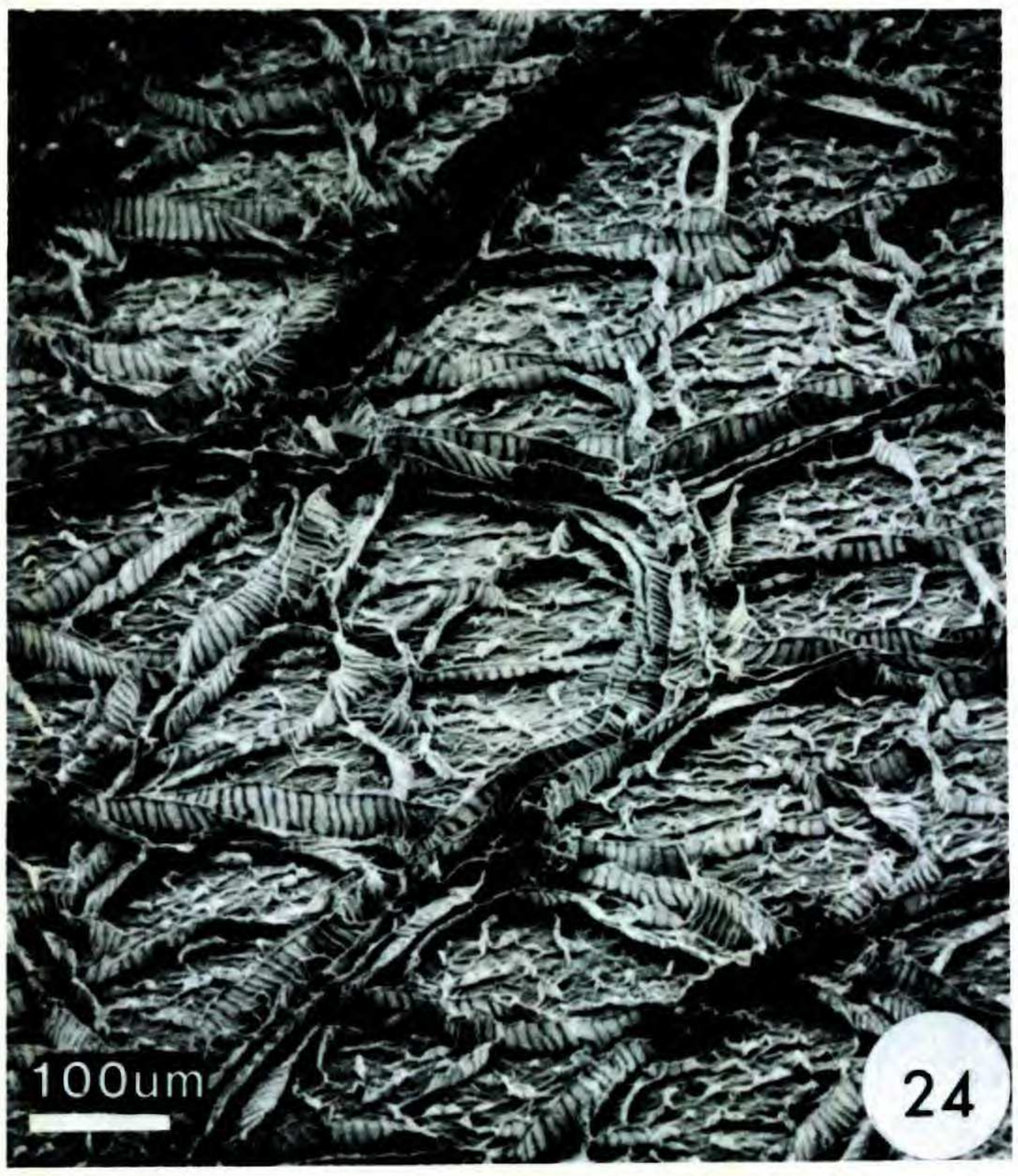

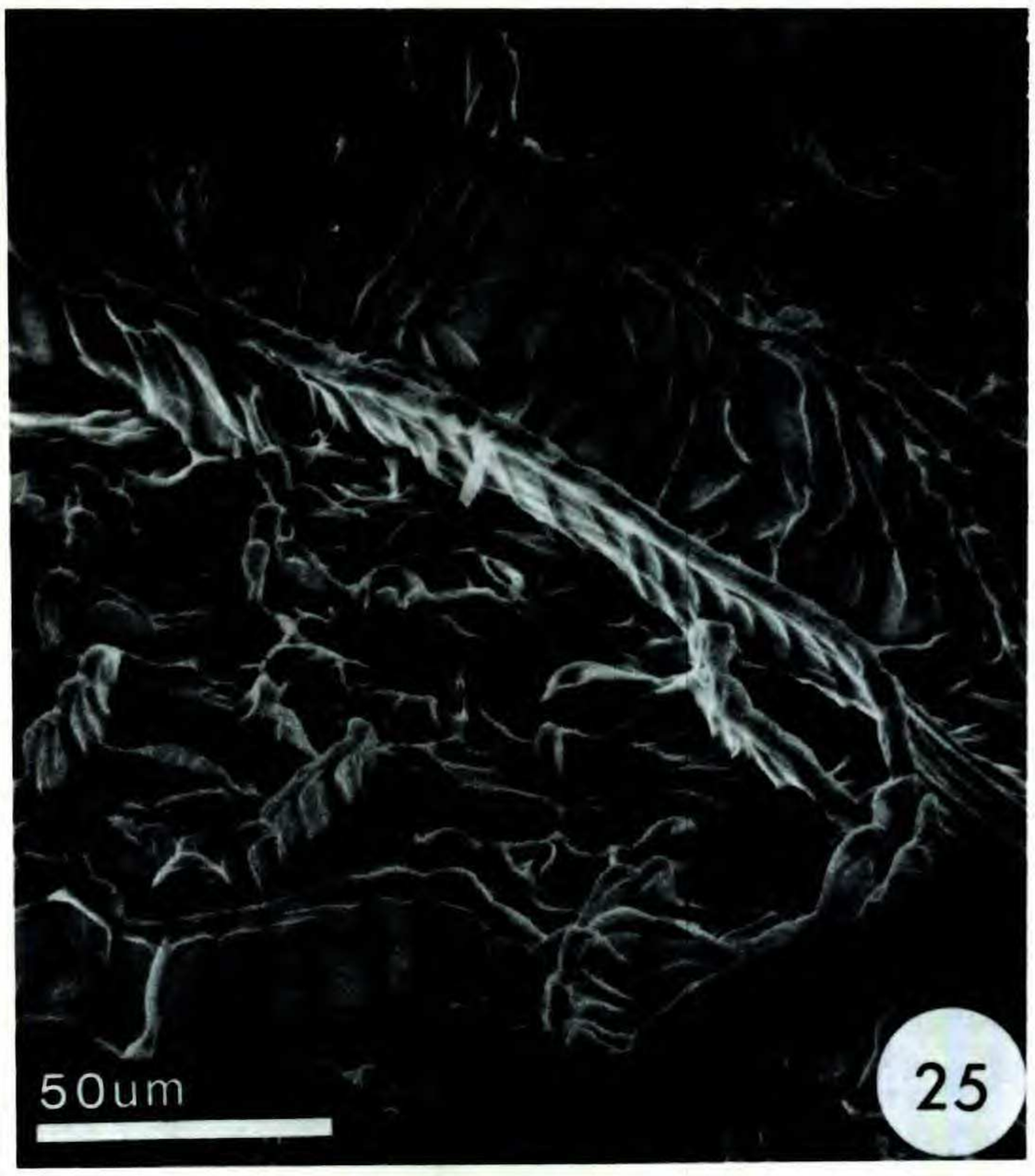

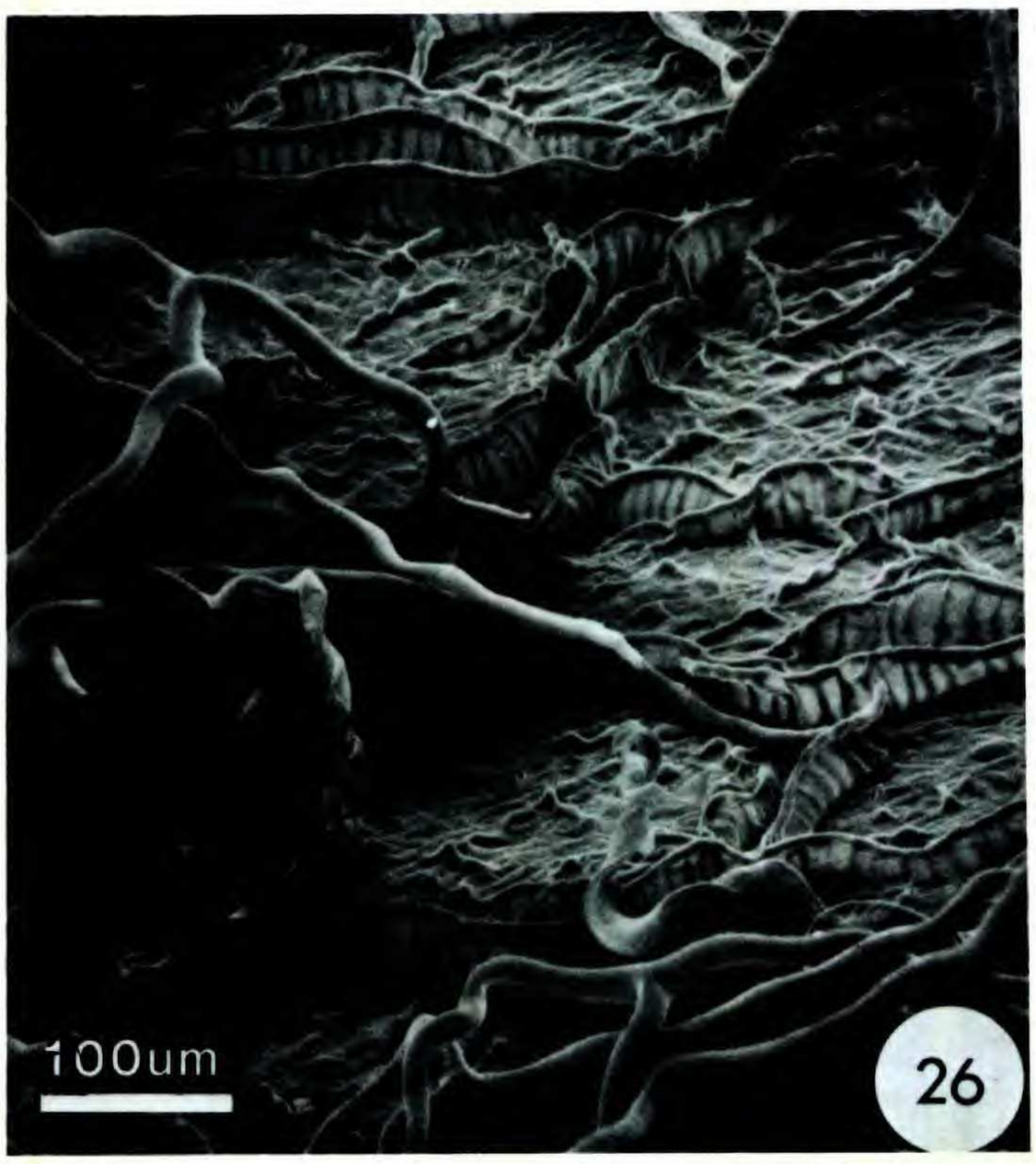

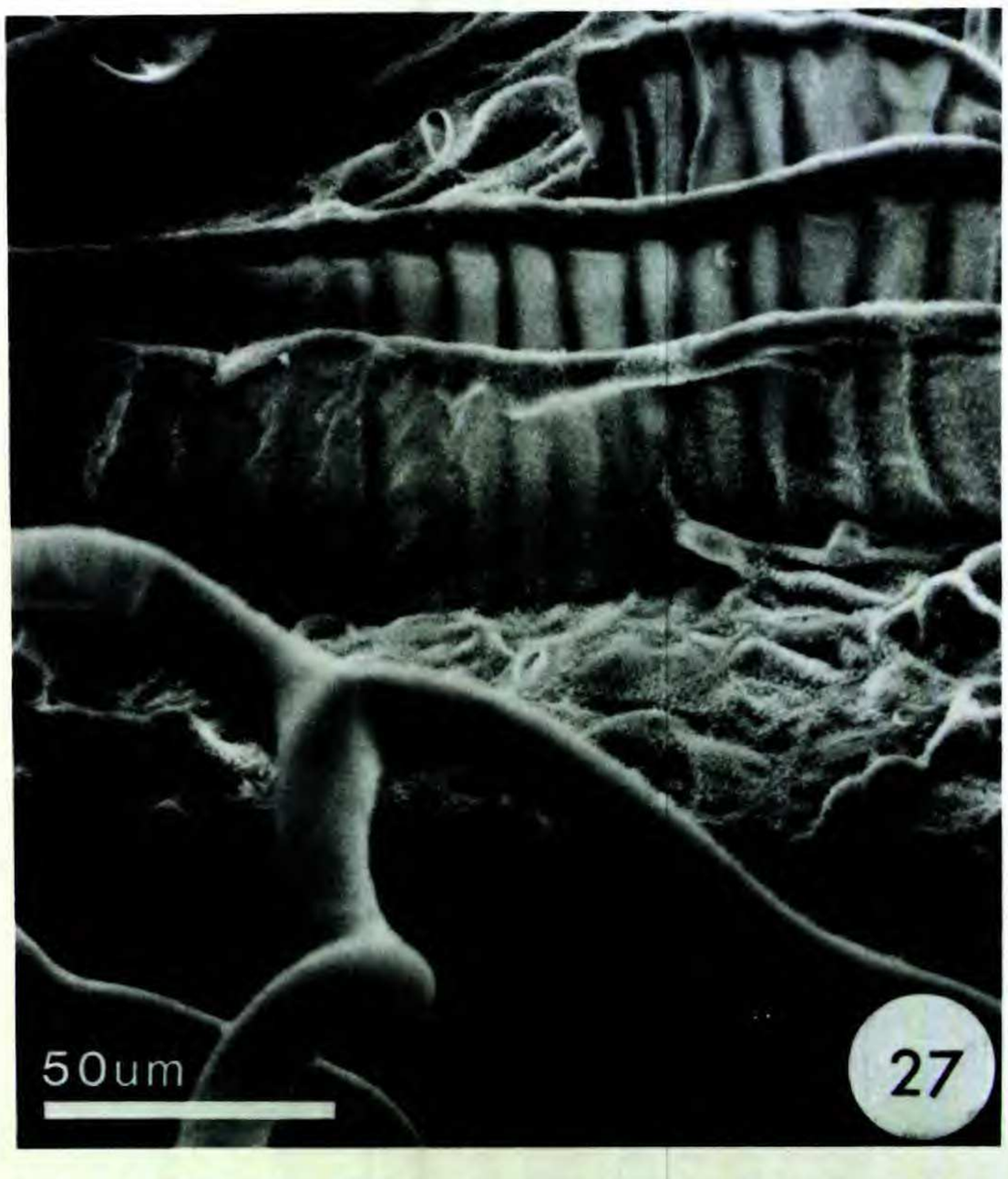

FIGURES 24–27. *SEM images, abaxial leaf surfaces of* Erythrina. *All images at 60° tilt.—24, 25. Lamellae,* E. stricta, *WA 74s897.—26, 27. Lamellae and two-armed hairs,* E. suberosa, *WA 75s960.*

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FIGURES 18–23. *Epidermal features of abaxial leaf surfaces of* Erythrina. *18, 20, 22.—SEM images. 19, 21, 23.—Anatomical sections.—18. Papillae,* E. guatemalensis, *PT 750419001.—19. Papillae,* E. folkersii, *PT 700010001.—20. Lamellae,* E. salviiflora, *PT 721346001.—21. Lamellae,* E. suberosa, *WA 75s960.—22. Glandular hair,* E. salviiflora, *PT 721346001.—23. "Glandular" hair, papillae, and lamellae,* E. berteroana, *WA 74s864.*

TABLE 18. *Comparison of leaf epidermal characters in* Erythrina *hybrids and parents.*

	Female Parent	F_1 Hybrid	Male Parent
	E. chiapasana PT 721005001	HO 82.278	*E. berteroana* PT 700044002
Figures	28–30	31–33	34–36
Hairs	dense covering of two-armed hairs	sparse two-armed hairs	hairs absent
Epidermal sculpturing	low ridges around stomata; no lamellae	open, irregular network of discontinuous lamellae; uneven in height, less than 15 μm tall	dense network of discontinuous lamellae, up to 40 μm tall
Epicuticular wax	wax absent	wax present	wax present
	E. guatemalensis PT 700018001	HO 82.289	*E. berteroana* PT 700044001
Figures	37–39	40–42	43–45
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	dense papillae, to 40 μm tall	sparse covering of papillae and 2–6-celled lamellae; short, less than 25 μm tall	dense network of discontinuous lamellae, to 40 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. guatemalensis PT 700018001	HO 82.283	*E. chiapasana* PT 721005001
Figures	46, 47	48, 49	50, 51
Hairs	hairs absent	sparse scattering of two-armed hairs	dense covering of two-armed hairs
Epidermal sculpturing	dense papillae to 40 μm tall	incipient papillae: low crescent-shaped ridges outlining anticlinal walls of epidermal cells	low ridges around stomata: no papillae
Epicuticular wax	wax present	wax present	wax absent
	E. guatemalensis PT 700018001	HO 82.647	*E. abyssinica* PT 731006002
Figures	52–54	55–57	58–60
Hairs	hairs absent	sparse covering of two-armed hairs	dense covering of two-armed hairs
Epidermal sculpturing	dense papillae to 40 μm tall	low epidermal ridges, less than 10 μm tall	low epidermal ridges, less than 10 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. guatemalensis WA 74c1453	HO 82.766	*E. senegalensis* WA 745100
Figures	61–63	64–66	67–69
Hairs	hairs absent	sparse scattering of balloon-like hairs, up to 50 μm × 100 μm in size	sparse scattering of balloonlike hairs, up to 50 μm × 100 μm in size
Epidermal sculpturing	dense papillae, to 40 μm tall	low, crescent-shaped epidermal ridges, less than 5 μm tall	low stellate papillae, less than 10 μm tall

TABLE 18. *Continued.*

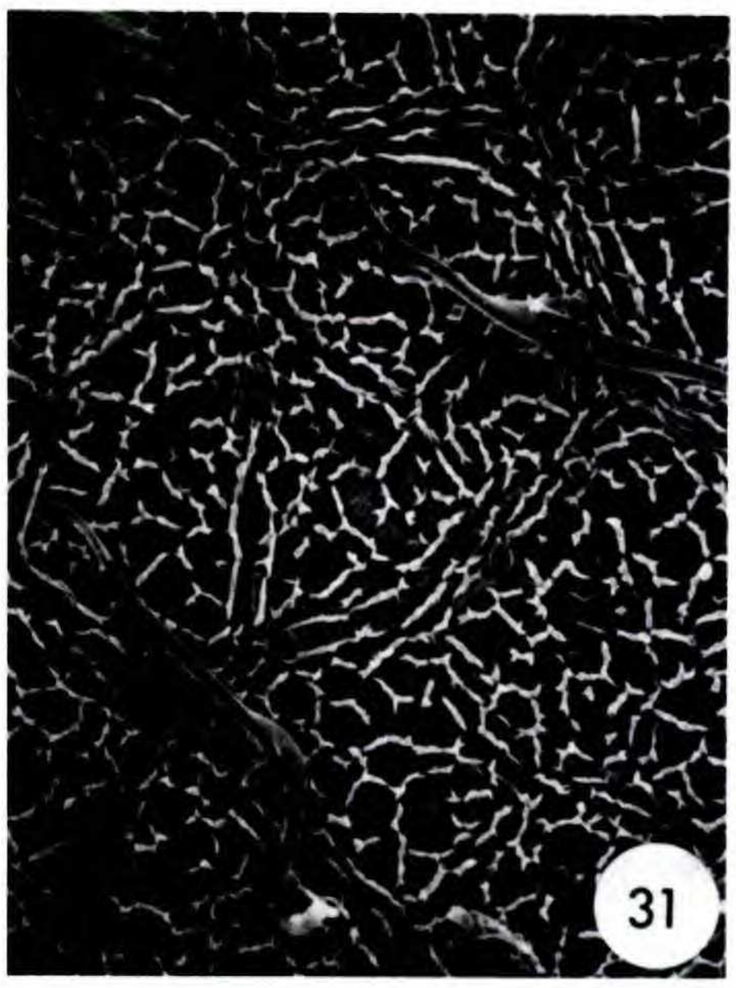
	Female Parent	F_1 Hybrid	Male Parent
Epicuticular wax	wax present	wax present	wax absent
	E. lysistemon PT 75028003	HO 84.238	*E. speciosa* PT 730708001
Figures	70, 71	72, 73	74, 75
Hairs	hairs absent	sparse scattering of two-armed hairs	sparse scattering of two-armed hairs
Epidermal sculpturing	low papillae, less than 10 μm tall	low epidermal ridges, less than 5 μm tall	low epidermal ridges, less than 5 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. crista-galli WA 74p840	(4 individuals)	*E. guatemalensis* WA 74c1453
Figures	76, 82	78–81, 84–87	77, 83
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	low, discontinuous lamellae, less than 10 μm tall, forming reticulate pattern	variable: papillae or discontinuous lamellae, to 15 μm tall	dense papillae, to 40 μm tall
Epicuticular wax	wax absent	wax present in all	wax present
	PT 840231		
	E. crista-galli WA 74p840	HO 84.235 (3 individuals)	*E. fusca* PT 74s99
Figures	88, 94	90–92, 96–98	89, 95
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	low discontinuous lamellae, less than 10 μm tall, forming reticulate pattern	variable: scattered low papillae, 3–4-celled lamellae or nearly flat	irregular convoluted surface with deep cavities, knobs, and protrusions
Epicuticular wax	wax absent	wax present in all	wax absent

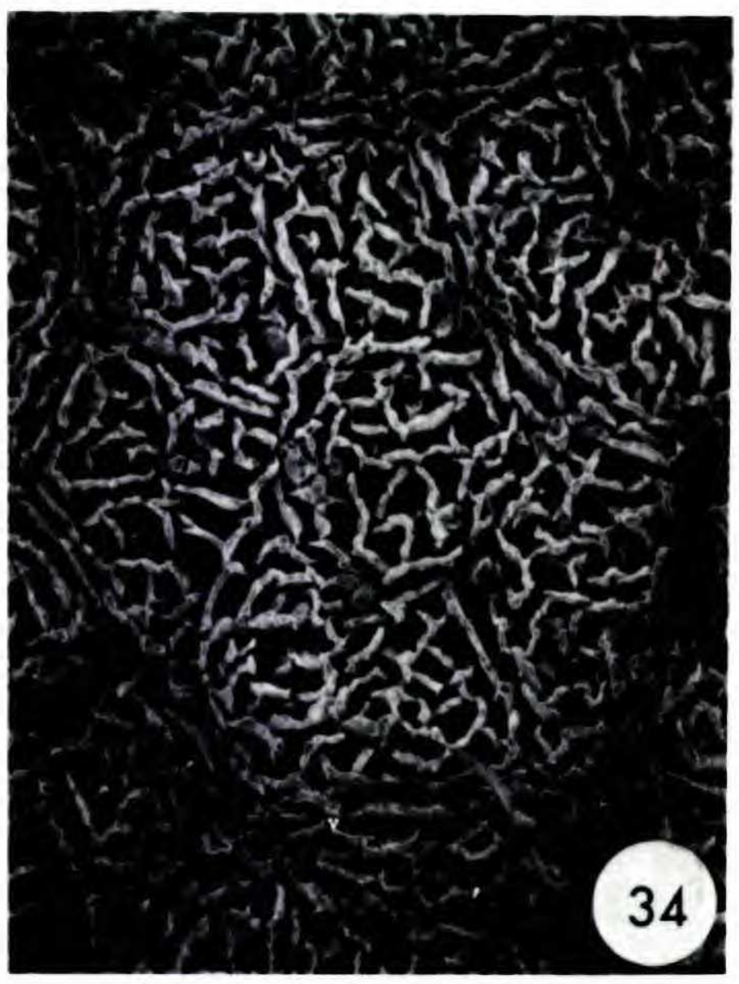
progeny in the F_2 generation. In the absence of large F_2 families, however, preliminary characterization of the inheritance of morphological characters can be obtained from F_1 hybrids.

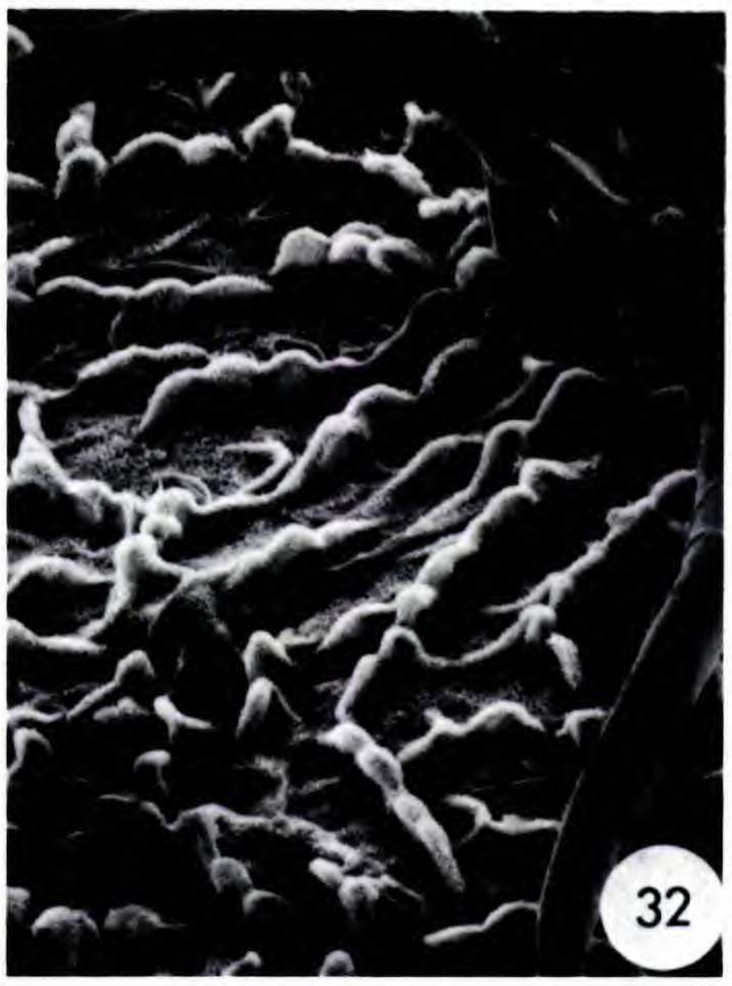
A study of the inheritance of phenetic traits in artificially produced hybrids serves several purposes beyond that of genetic analysis. Firstly, it allows for confirmation of hybridity in the hybrid progeny. In any experimental hybridization, there exists the possibility that the cross may be spurious; the progeny could result from contamination of self-pollen on the stigma, or from agamospermy. However, if the progeny possess a character present in the male parent but absent in the female, their hybrid nature is reasonably confirmed.

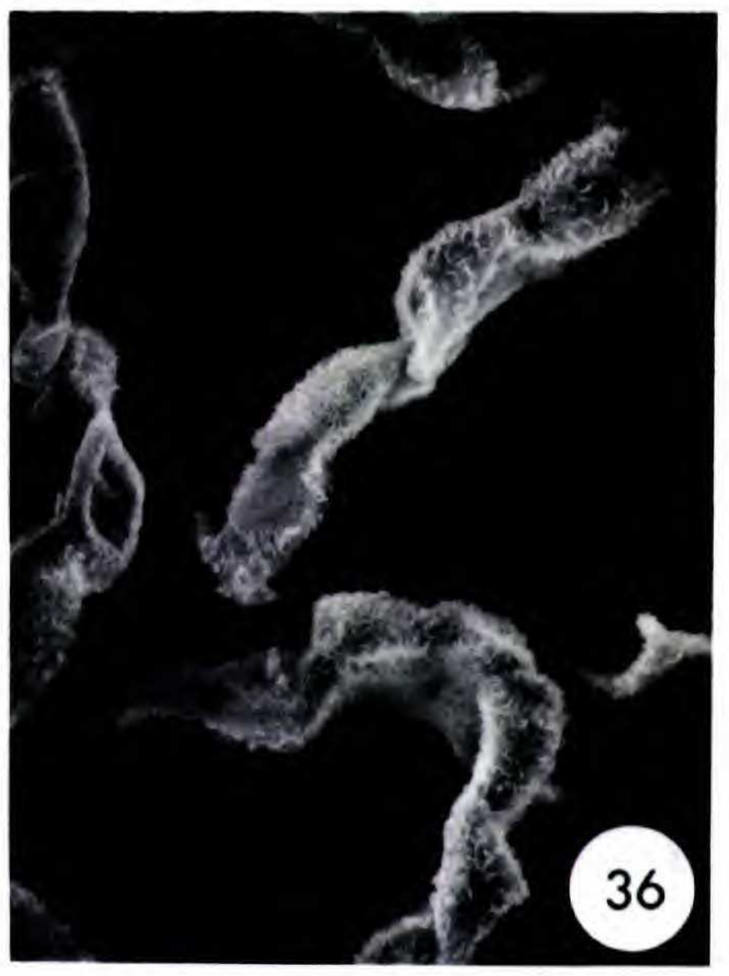
A second purpose for studying the inheritance of morphological traits in artificial hybrids is to generate information on the patterns of variation to be expected when hybridization occurs in nature. If, as Raven (1980) and Grant (1981) have suggested, there is a great deal of hybridization in flowering plants that passes undetected as such, then study of the products of artificial hybridization may help in the discovery and confirmation of hybrids in natural populations. This method was used effectively, for example, by Nobs (1963) in his biosystematic study of *Ceanothus*. Some of the artificial F_2 hybrid segregates of *Ceanothus* closely resembled stabilized populations with restricted ranges recognized as species. Nobs used this evidence to support his hypothesis that these species were of hybrid origin and were derived from pairs of extant, more wide-ranging species.

A similar study, combining artificial hybridization and analysis of natural hybridization, conducted by Gillett & Lim (1970) on *Bidens* in

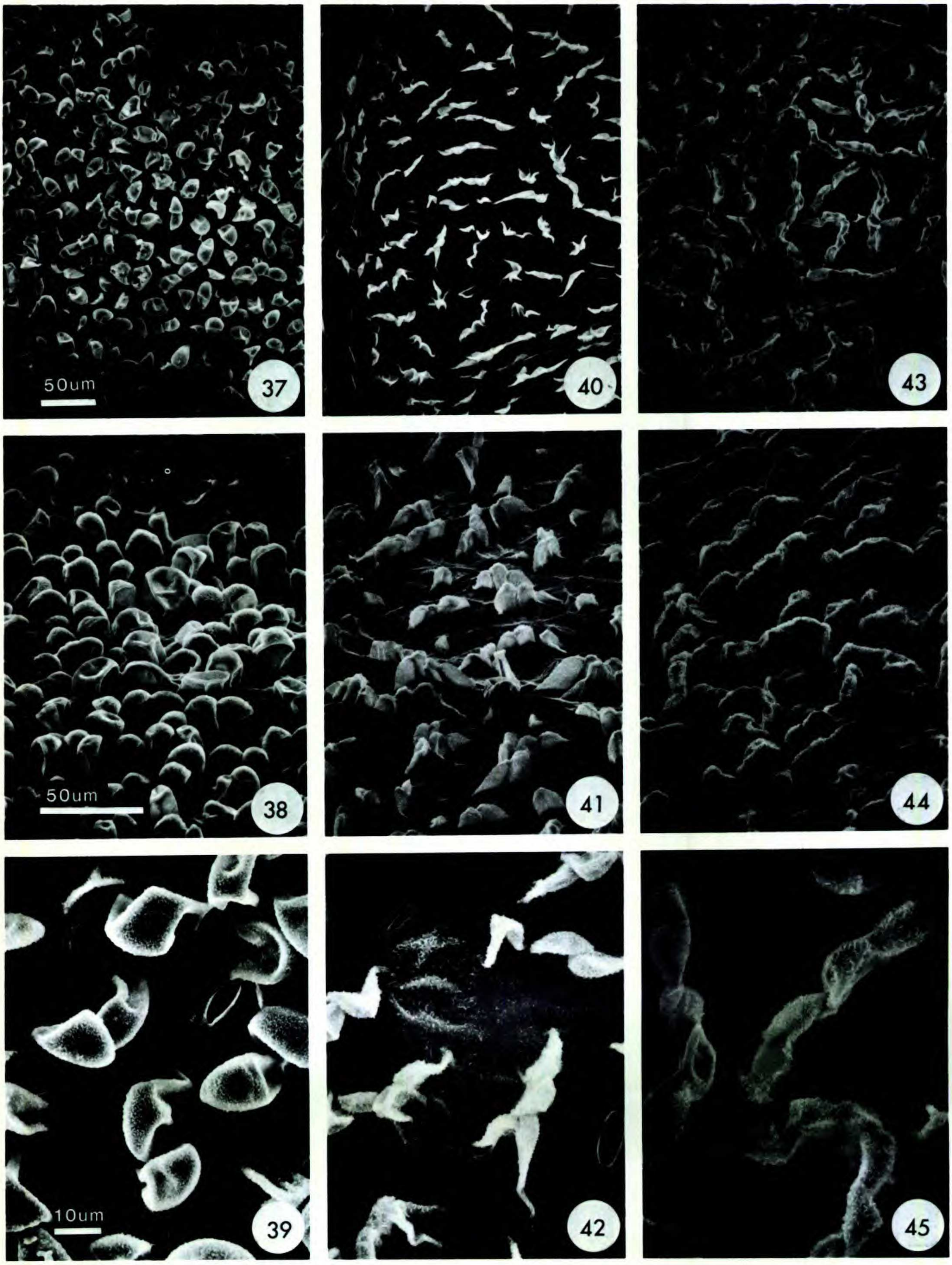




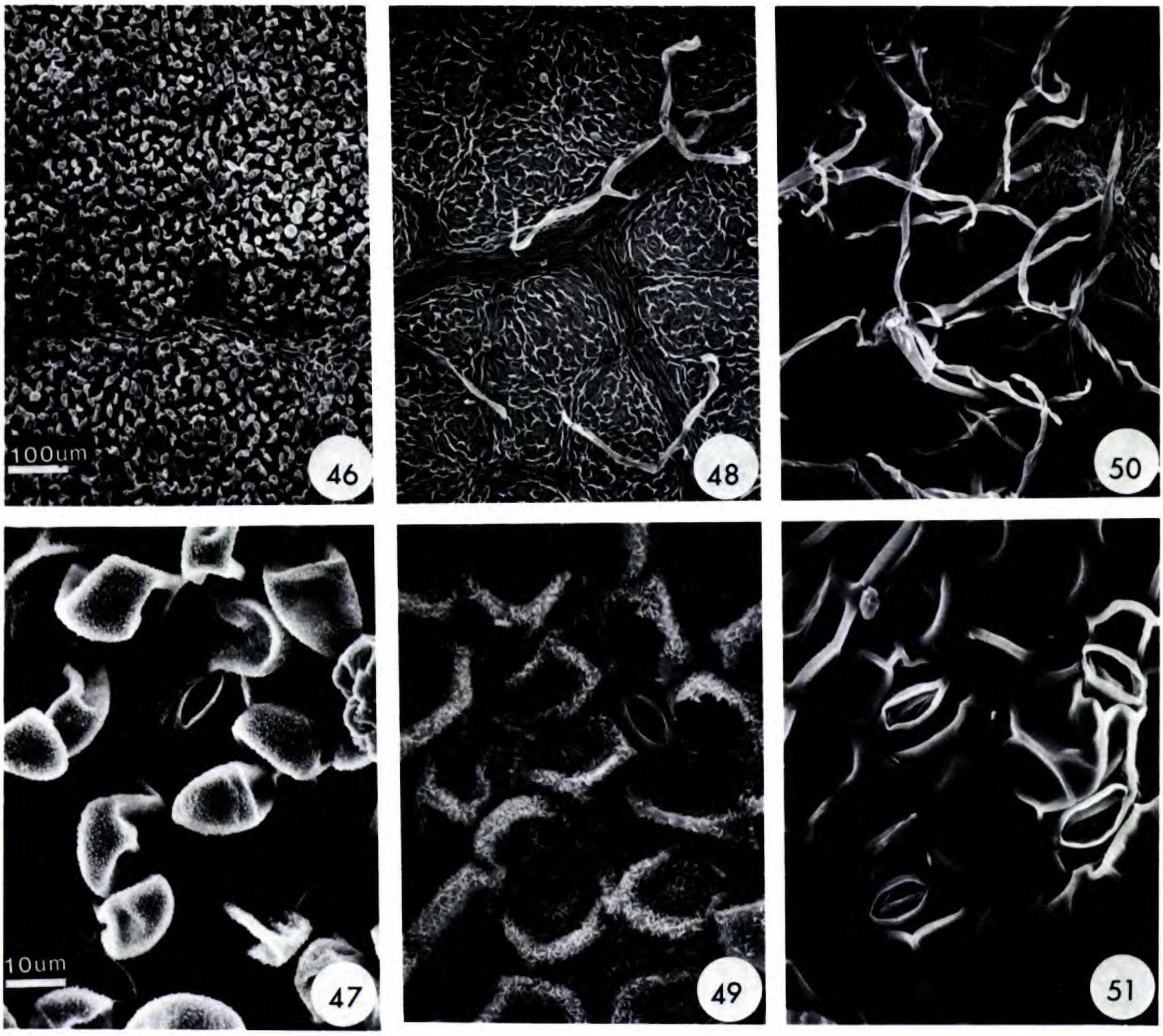




FIGURES 28–36. *SEM images, abaxial leaf surfaces of* Erythrina chiapasana × E. berteroana *and parents. Each horizontal row at equal magnification. 29, 32, 35 at 60° tilt.—28–30.* E. chiapasana, *PT 721005001, female parent.—31–33.* E. chiapasana × E. berteroana, *HO 82.278.—34–36.* E. berteroana, *PT 700044002, male parent.*



FIGURES 37–45. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. berteroana *and parents. Each horizontal row at equal magnification. 38, 41, 45 at 60° tilt.—37–39.* E. guatemalensis, *PT 700018001, female parent.—40–42.* E. guatemalensis × E. berteroana, *HO 82.289.—43–45.* E. berteroana, *PT 700044001, male parent.*



FIGURES 46–51. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. chiapasana *and parents. Each horizontal row at equal magnification.—46, 47.* E. guatemalensis, *PT 700018001, female parent.—48, 49.* E. guatemalensis × E. chiapasana, *HO 82.283.—50, 51.* E. chiapasana, *PT 721005001, male parent.*

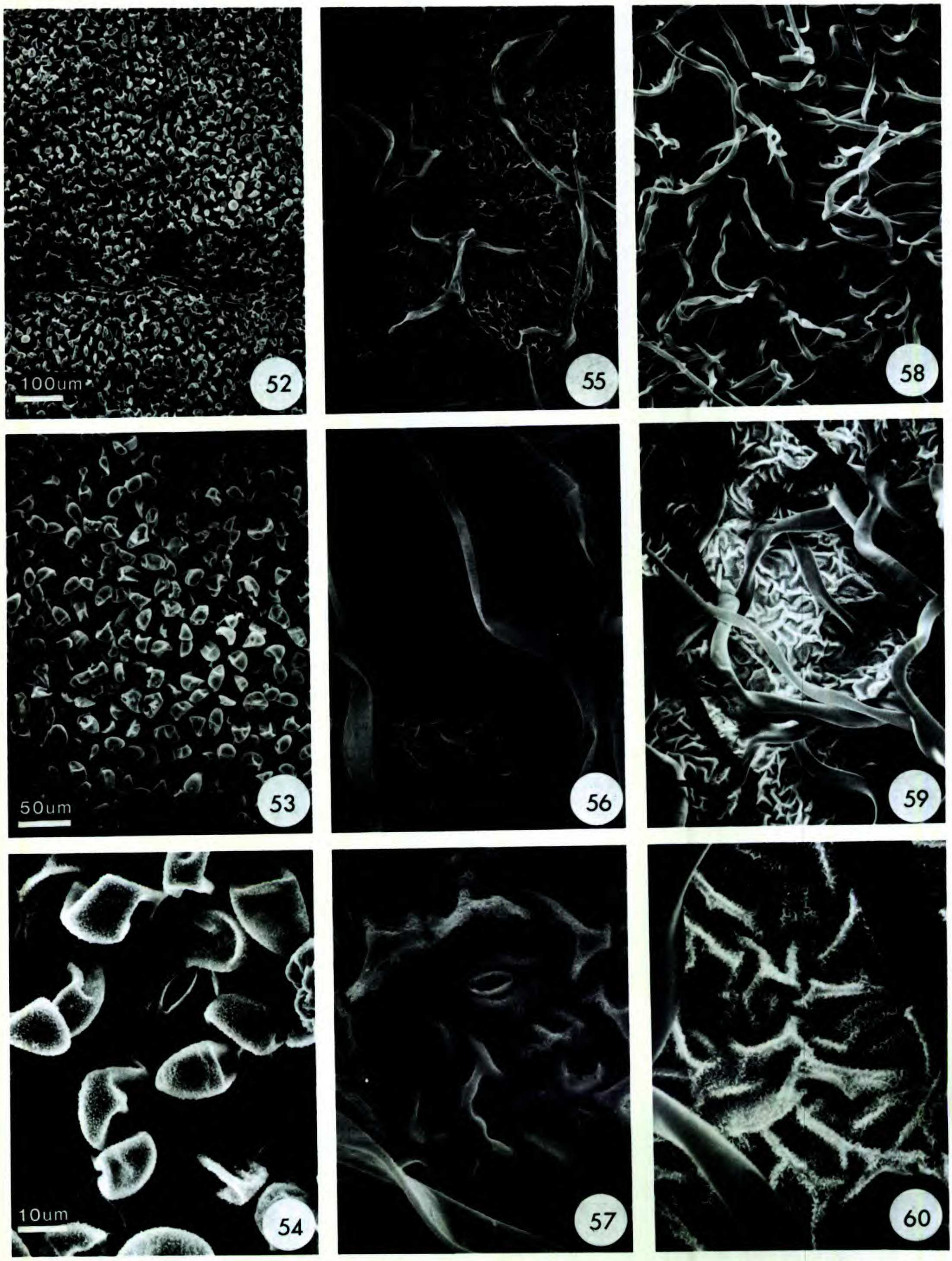
Hawaii, has been questioned by Ganders & Nagata (1984). They showed that some of the putative natural hybrids were merely intraspecific variants, and Ganders & Nagata concluded that adaptive divergence was more important than hybridization in the evolution of *Bidens* in the Hawaiian Islands. Although all of the 17 Hawaiian *Bidens* species are in fact interfertile, natural hybridization is rare because they are mostly allopatric. Evidently Gillett & Lim used too few characters and ignored intrapopulation variation. An important caveat is to avoid a too facile interpretation of hybridization results when applying them to the study of processes in nature.

In this research, two sets of phenetic traits were examined in the *Erythrina* hybrids and their parent species: 1) features of the epidermis of abaxial leaf surfaces, and 2) morphology and color of the flowers.

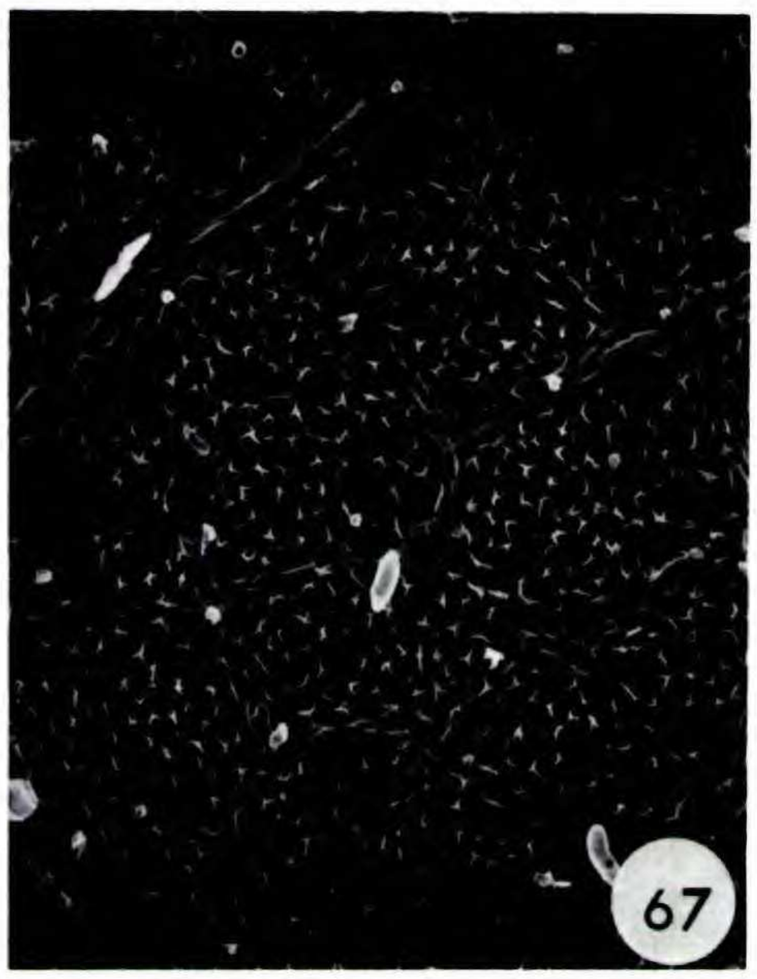
EPIDERMAL FEATURES OF *ERYTHRINA* LEAVES

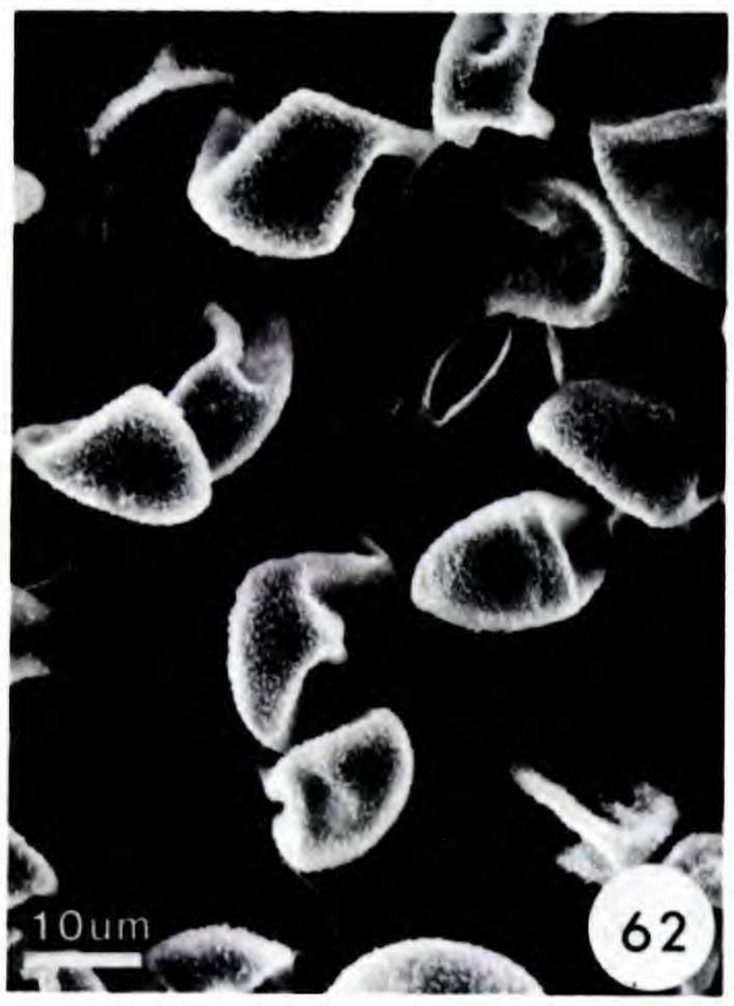
Characters of the leaf are second only to those of flowers in their use and value in taxonomic studies (Stace, 1984). Studies of the inheritance of leaf surface characters in interspecific hybrids have recently been carried out in *Aloe* and *Gasteria* (Liliaceae) (Cutler, 1972), in *Ilex* (Baas, 1978), and in *Quercus* (Cottam et al., 1982).

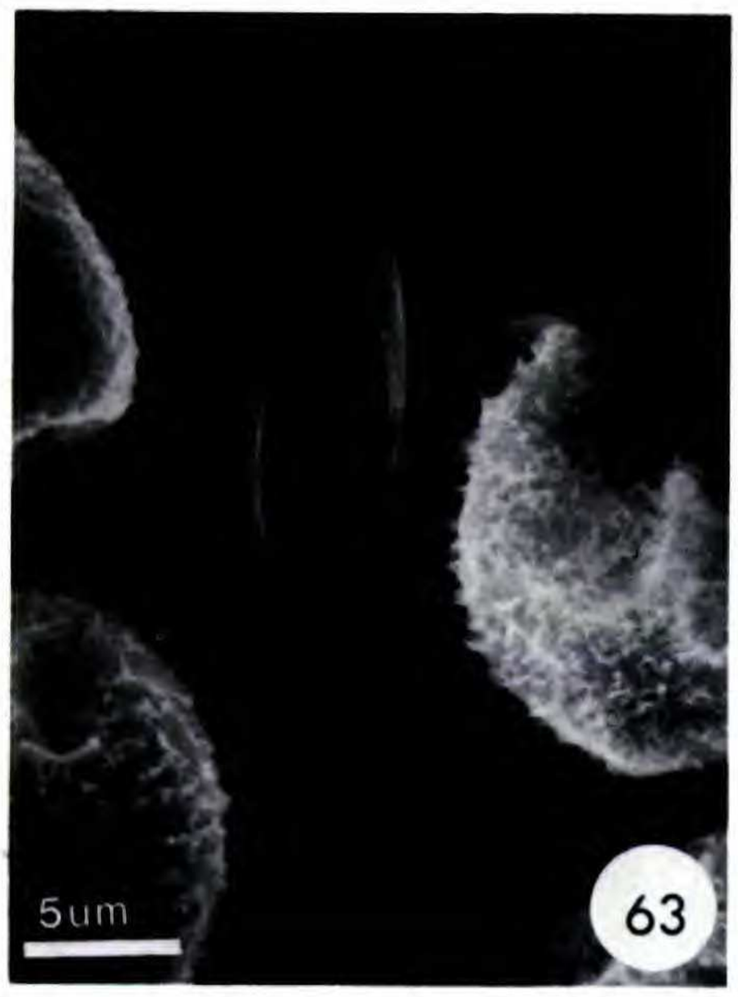
Erythrina species possess a wide variety of leaf surface characters. These have figured prominently in the taxonomic delimitation of the species (Krukoff, 1939a, b; Krukoff & Barneby, 1974). In these previous works the surface characters



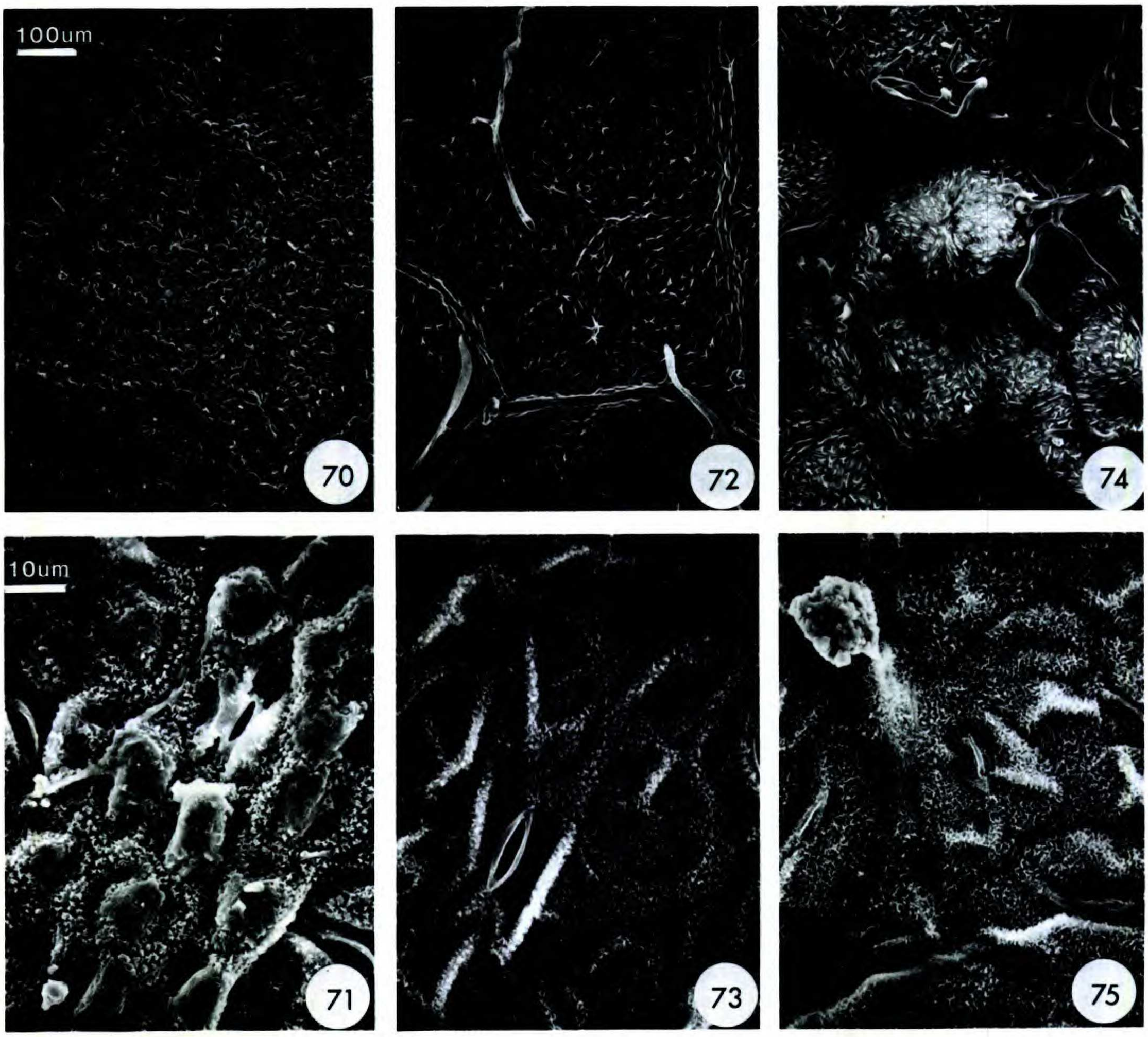
FIGURES 52–60. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. abyssinica *and parents. Each horizontal row at equal magnification.—52–54.* E. guatemalensis, *PT 700018001, female parent.—55–57.* E. guatemalensis × E. abyssinica, *HO 82.647.—58–60.* E. abyssinica, *PT 731006002, male parent.*







FIGURES 61–69. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. senegalensis *and parents. Each horizontal row at equal magnification.—61–63.* E. guatemalensis, *WA 74c1453, female parent.—64–66.* E. guatemalensis × E. senegalensis, *HO 82.766.—67–69.* E. senegalensis, *WA 74s100, male parent.*



FIGURES 70–75. *SEM images, abaxial leaf surfaces of* Erythrina lysistemon × E. speciosa *and parents. Each horizontal row at equal magnification.—70, 71.* E. lysistemon, *PT 750280003, female parent.—72, 73.* E. lysistemon × E. speciosa, *HO 84.283.—74, 75.* E. speciosa, *PT 730708001, male parent.*

were not studied with high magnification or anatomical sectioning, however, and the structure of some of the surface characters was misinterpreted. This is discussed below in the description of epidermal characters. Leaf epidermal features of a few species of *Erythrina* have also been surveyed using scanning electron microscopy (Ayensu, 1977).

Materials and Methods

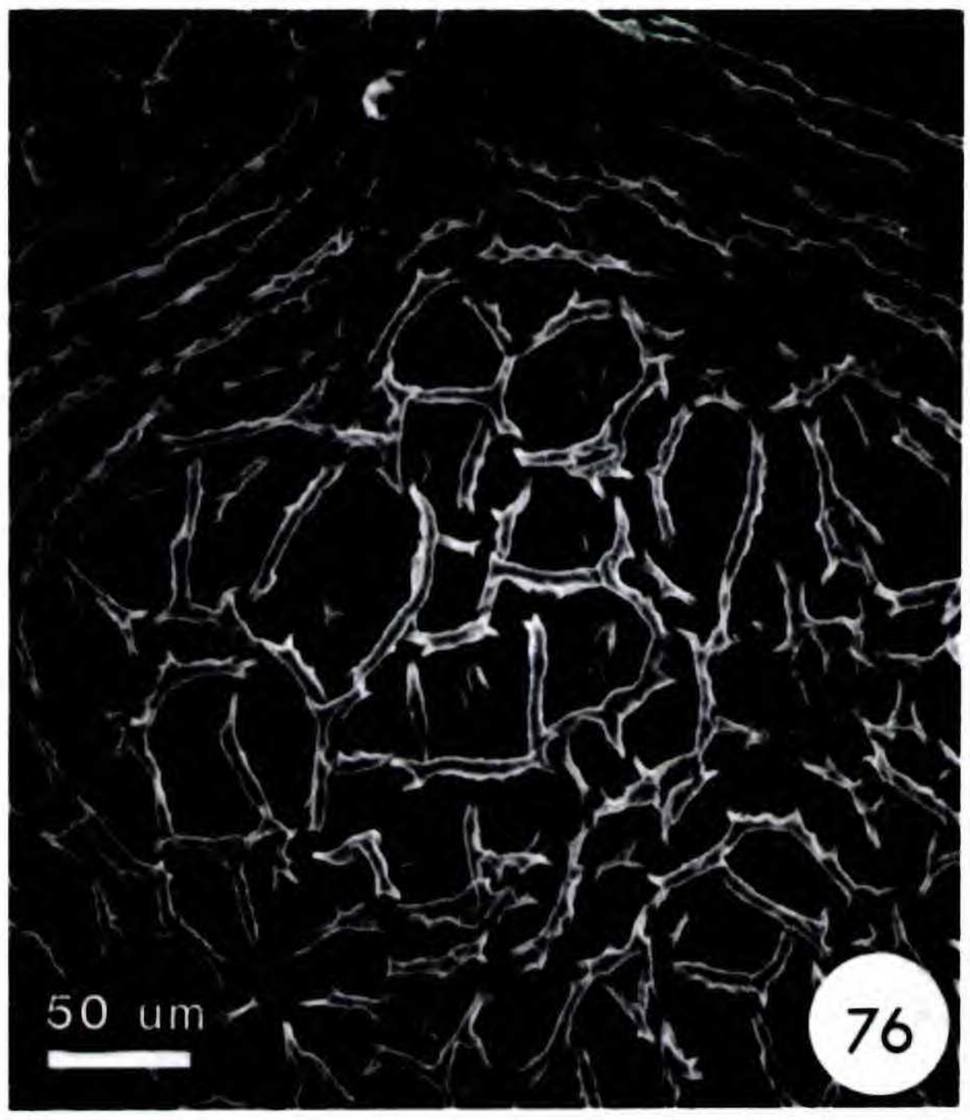
In this study, only the abaxial surfaces of leaves were examined. All samples were obtained from mature, fully expanded leaves, which were pressed and dried as in preparation of herbarium specimens. The specimens were gold-coated with a Polaron E5000 sputter-coater and observed with an Hitachi 450-S scanning electron microscope. For a few selected species, anatomical sections of paraffin-embedded leaves were prepared by Dr. Hiroshi Tobe of Chiba University, Japan.

Results

Survey of Leaf Epidermal Features in Erythrina

Epicuticular Wax. Platelets of epicuticular wax cover the abaxial leaf surfaces of many *Erythrina* species. The wax gives a whitish, glaucous appearance to the leaf observed without magnification. The platelets are 1–3 μm in size, are oriented randomly on the leaf surface, and vary in density (Figs. 12, 13). Epicuticular wax is consistently present in some species, but in others its presence or absence is variable even among individuals of a single population.

Multicellular Branched Hairs. Several types of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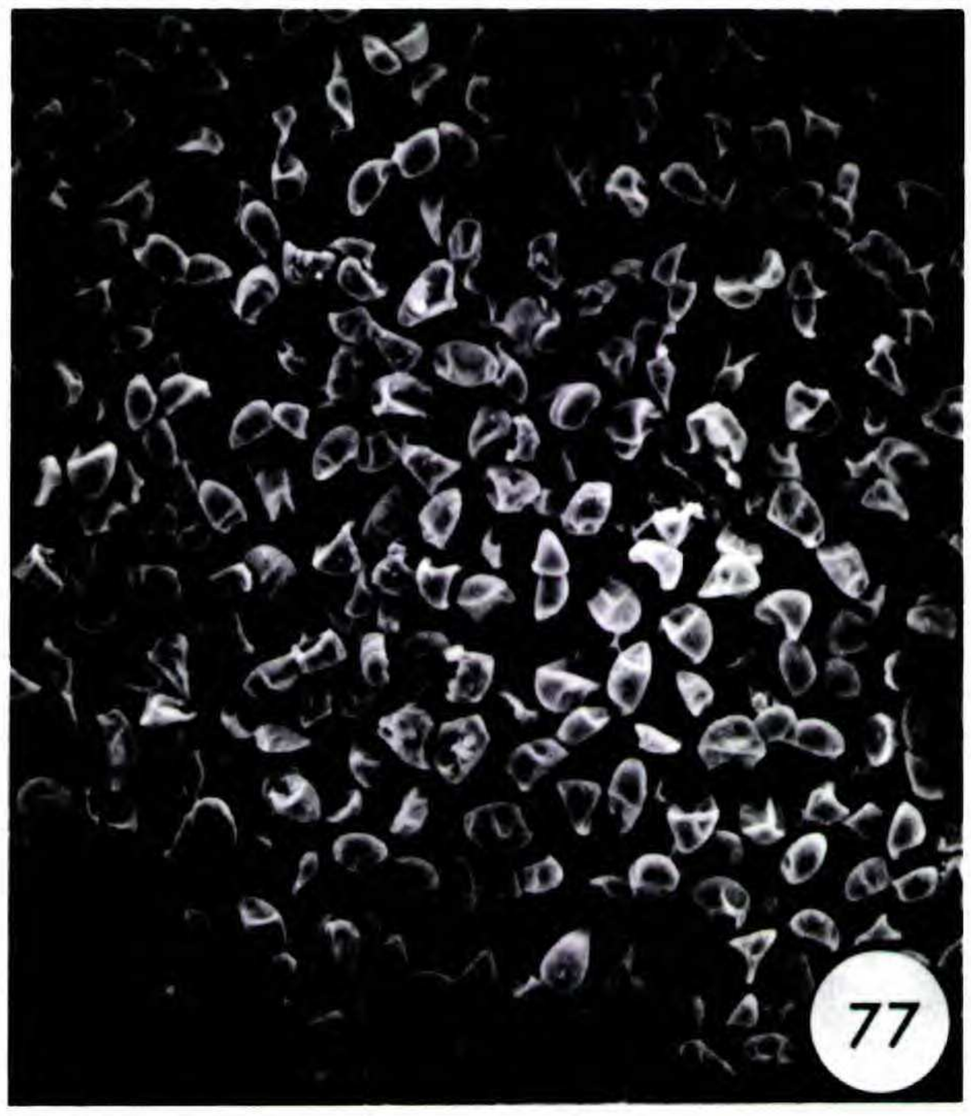
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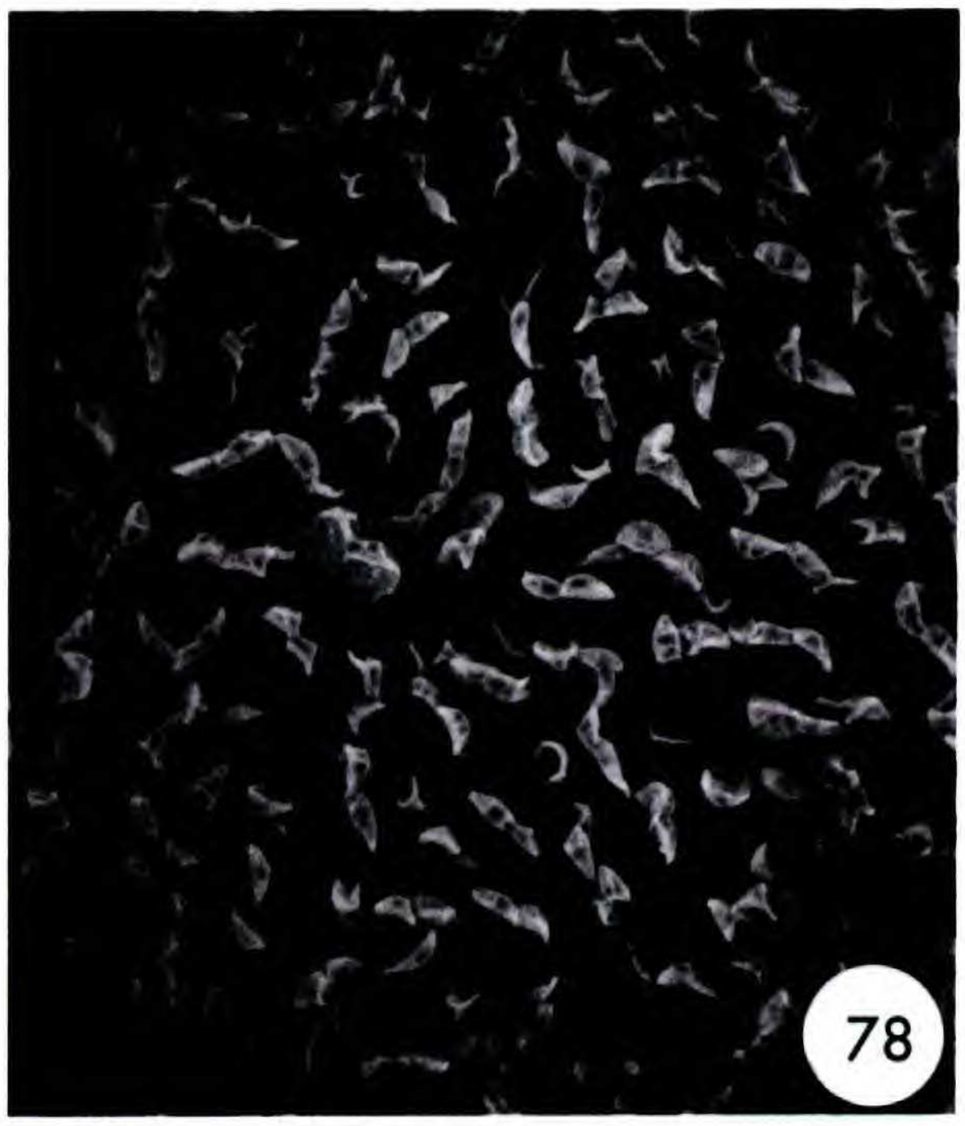
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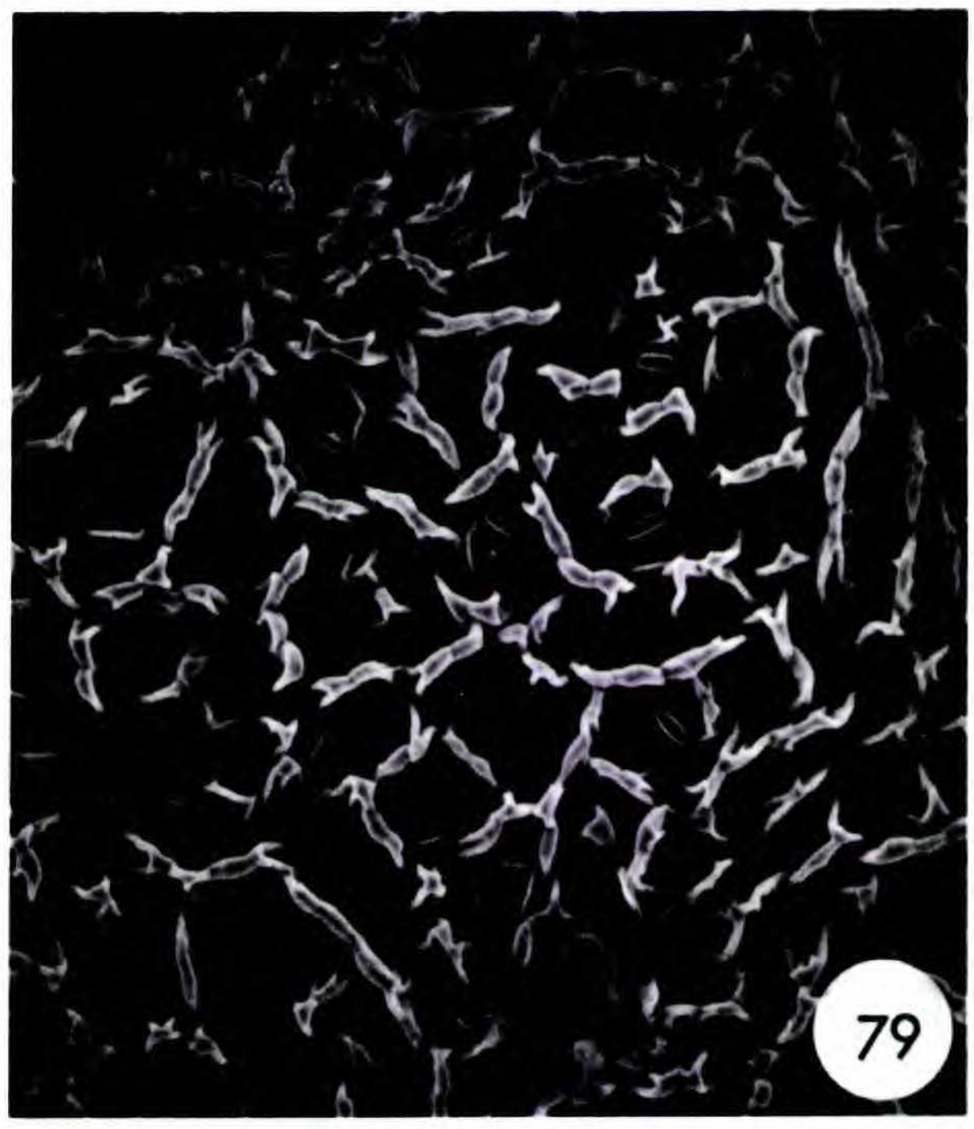
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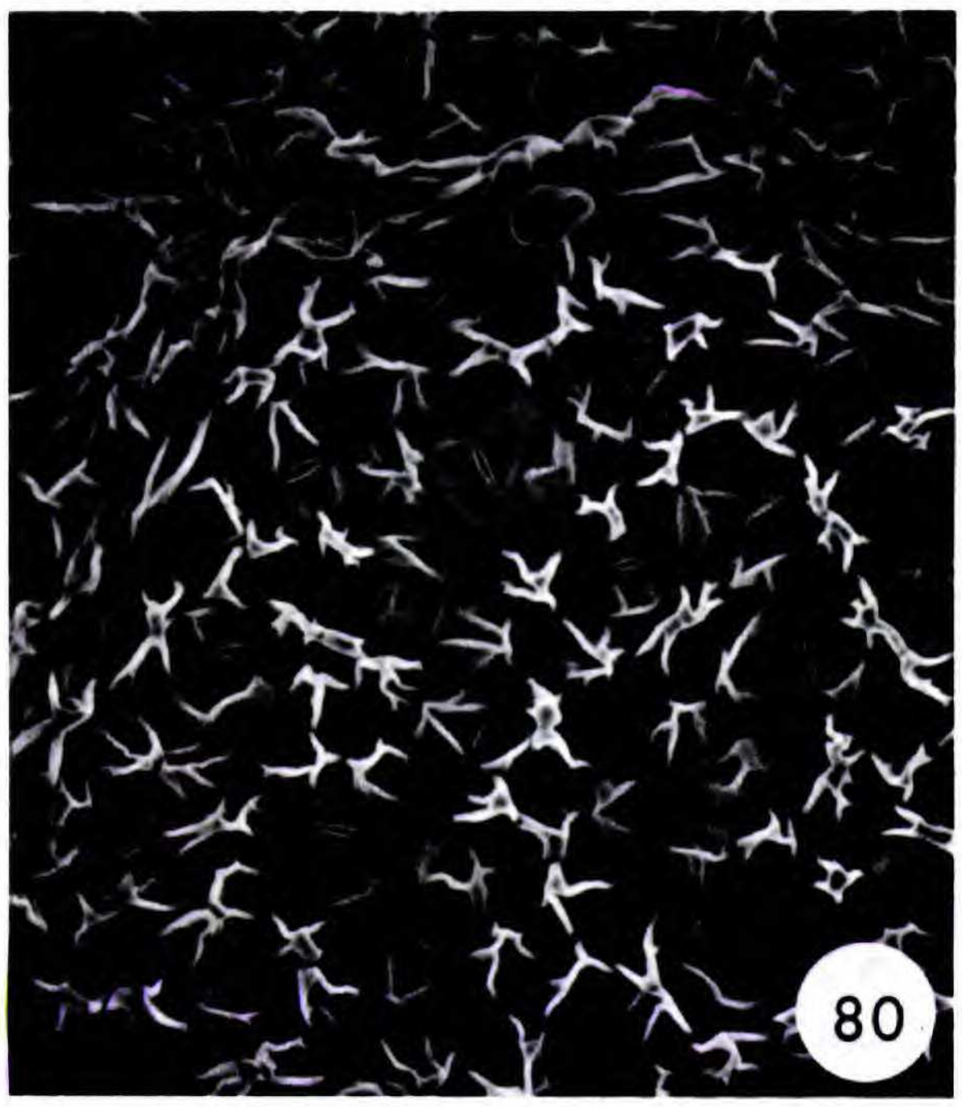
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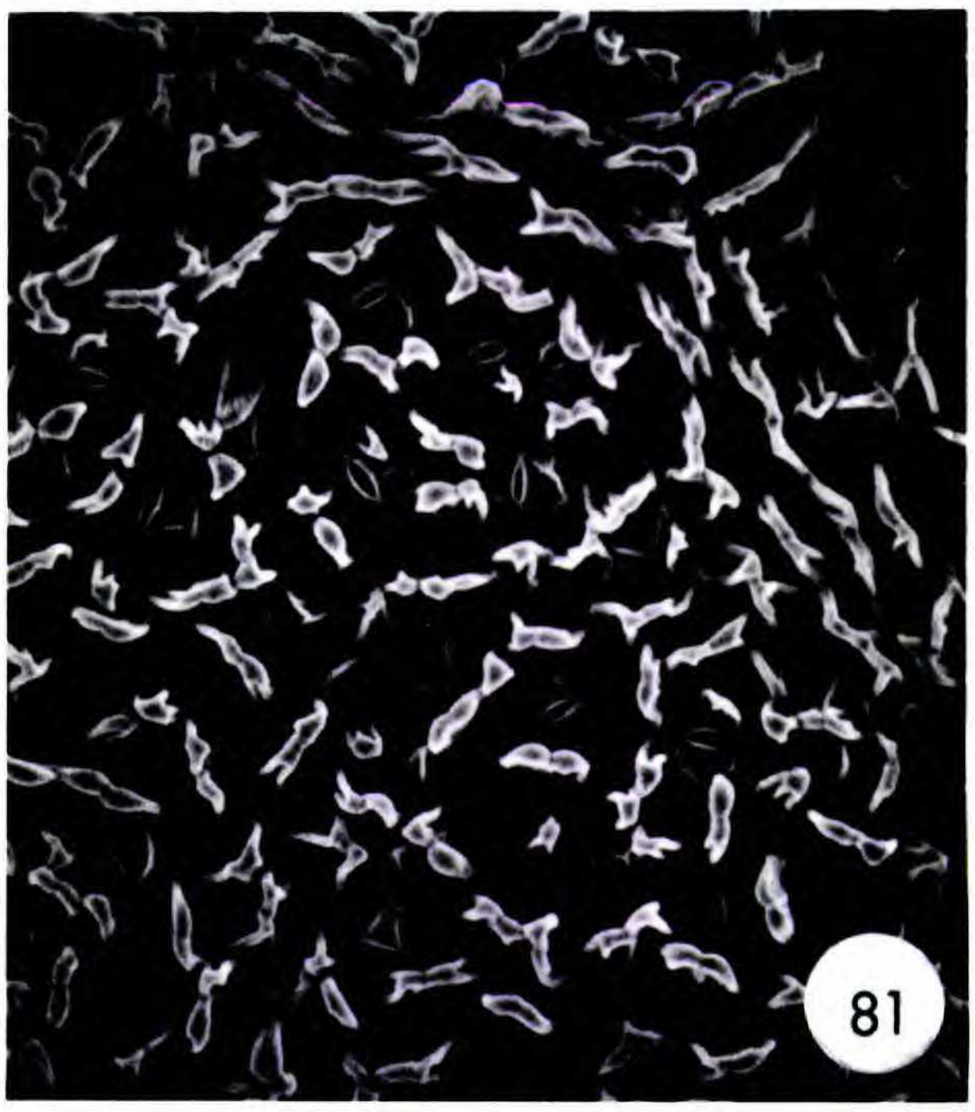
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hair occur on the abaxial leaf surfaces of *Erythrina* species. The most common, and the only type found in sect. *Erythrina*, is a multicellular, two-armed hair (Fig. 14). This consists of several short basal cells, one or two longer cells forming the stalk, and one cell forming each of the arms, which may be 1,000 μm or more in length. Two-armed hairs are present on the young leaves of most species in sect. *Erythrina* and in species of other sections as well, but in many species they are deciduous and are absent from fully expanded leaves. In the other species, the hairs are retained on mature leaves and form a dense tomentum.

Multiple-branched, dendritic hairs (Fig. 15) are restricted to sect. *Erythraster*. They occur in all species of that section and are found on calyces, inflorescence branches, and on leaves. Each branch of the dendritic hair is 50–100 μm long and is formed by a single cell. The dendritic hair has about 8–12 branches and extends up to 300 μm above the surface of the epidermis.

"Glandular" Hairs. Multicellular, uniseriate hairs occur sporadically on leaf surfaces of many *Erythrina* species (Figs. 22, 23). They appear to be glandular, but what substance these hairs secrete, if any, is not known. They are squat, rounded hairs about 50 μm long and comprised of five or six cells. Observed with a microscope, they glisten with a translucent amber color.

Unicellular Hairs. The most common type of multicellular hair in *Erythrina* is formed by a rounded or elliptic, thin-walled cell which loses its cytoplasm and collapses at leaf maturity or upon drying (Fig. 16). These I refer to as "balloonlike" hairs. They occur in several sections of *Erythrina*. Long, flat, ribbonlike hairs 500 μm or more in length are found particularly along the principal veins of the leaf in some species (Fig. 17). This type of hair is predominant in the Mexican sects. *Breviflorae* and *Leptorhizae*.

Epidermal Sculpturing: Papillae and Lamellae. The remaining types of *Erythrina* trichomes are considered separately from hairs because they are more integrally a part of the foliar epidermis. These are papillae and lamellae, which I refer to collectively as "epidermal sculpturing."

Papillae are single-celled, fingerlike trichomes. Each papilla is formed by the protrusion of an epidermal cell above the leaf surface. Papillae are up to 40 μm tall and 15 μm in diameter (Figs. 18, 19). Papillae and the epidermal surface between them are usually covered with epicuticular wax platelets. Under low magnification, a leaf surface with papillae appears covered with whitish granules. Krukoff (Krukoff & Barneby, 1974) termed such leaf surfaces "farinose-ceriferous" or "granular-ceriferous," but the "granules" he described are wax-covered papillate cells, not individual particles of wax.

Papillae similar to the ones found in *Erythrina* occur on leaf surfaces in many groups of plants, but the structures I have termed "lamellae" have not to my knowledge been reported from leaf epidermis of any angiosperm besides *Erythrina*. Lamellae, like papillae, are formed by protrusions of epidermal cells, but in lamellae the cells are joined edge-to-edge to form continuous "walls" one cell thick that stand above the surface of the leaf (Figs. 20, 21). Leaf surfaces with lamellae are also usually covered with epicuticular wax.

Lamellae occur in several species of sect. *Erythrina*. In these species the lamellae are discontinuous; each lamella is composed of several to twenty cells standing edge-to-edge. The lamellae form a dense, discontinuous network with a characteristic pattern when observed at low magnification (Fig. 34). Krukoff (Krukoff & Barneby, 1974) referred to leaves with wax-covered lamellae as "reticulately ceriferous."

A unique pattern of lamellae occurs only in the Asian sect. *Suberosae* (Figs. 24–27). The lamellae are tall (50 μm) and continuous. Parallel rows of several lamellae, each leaning at a different angle with respect to the leaf surface (Fig. 25), are joined to form an open network of interconnected polygons (Fig. 24). Shorter lamellae extend into the center of the polygons. The distribution of the polygons is associated with the vascular tissue of the leaf. *Erythrina suberosa* (Figs. 26, 27) has both polygon-forming lamellae and two-branched hairs.

Trichome characters are generally quite constant within a species and are useful taxonomic markers, often allowing species identification from

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FIGURES 76–81. *SEM images, abaxial leaf surfaces of* E. crista-galli × E. guatemalensis *and parents. All photos at equal magnification.—76.* E. crista-galli, *WA 74p840, female parent.—77.* E. guatemalensis, *WA 74c1453, male parent.—78–81.* E. crista-galli × E. guatemalensis, *four F_1 siblings, PT 820548 and WA 82.278.*

sterile material. In contrast, presence or absence of epicuticular wax is variable within populations and is not a useful marker. As will be seen in the discussion of the hybrids below, epicuticular wax is evidently a simply inherited trait. Krukoff (Krukoff & Barneby, 1973) separated the Mexican species *Erythrina americana* Miller and *E. coralloides* A. DC. (sect. *Erythrina*) solely on the basis of presence or absence of epicuticular wax. This trait is variable and is not well correlated with geographic distribution. For this and other reasons, *Erythrina coralloides* is here considered a synonym of *E. americana*.

Inheritance of Leaf-Surface Characters in Interspecific Hybrids

Each of the six plates comprising Figures 28–75 illustrates the leaf surface features of a single F_1 hybrid and its two parents. On each plate, the female parent is illustrated on the left, the male parent on the right, and the hybrid in the center. Each horizontal row of photographs is a comparison of the three individuals at equal magnification (indicated by the bar in the left-hand photograph). Table 18 summarizes the features present in the parents and hybrids.

Four of the six hybrids illustrated were derived from the same genetic individual as female parent, *Erythrina guatemalensis* PT 700018001 and WA 74c1453. It is particularly instructive to note the pattern of inheritance in the hybrids produced from the combination of this genome with those of four different species: *E. berteroana*, *E. chiapasana*, *E. abyssinica*, and *E. senegalensis*.

Erythrina guatemalensis has well-developed papillae on the abaxial leaf surface, each composed of a single epidermal cell; the male parent *E. berteroana* has well-developed lamellae, each composed of about 4–5 cells forming a "wall-like" structure. The F_1 hybrid has lamellae intermediate in length between the two parents, composed of 2–3 cells, but these are lower in stature and less developed than the epidermal sculpturing of either parent (Figs. 37–45).

Erythrina guatemalensis lacks hairs on mature leaf surfaces. The male parents *E. chiapasana* and *E. abyssinica* have dense covering of two-armed hairs. The hybrids derived from these males with *E. guatemalensis* as female also possess two-armed hairs, but at a much lower density than in the male parents (Figs. 46–51, 52–60). *Erythrina senegalensis* has scattered balloonlike hairs, and these are also inherited in the F_1 hybrid *E. guatemalensis* × *E. senegalensis* (Figs. 61–69). The male parents *E. chiapasana* and *E. senegalensis* lack epicuticular wax; this trait is present in the female *E. guatemalensis* and in the hybrids. (Other individuals of *E. chiapasana* than the one used in this cross do have epicuticular wax.)

Similar patterns of inheritance are exhibited by the other F_1 hybrids, for example, *Erythrina chiapasana* × *E. berteroana* (Figs. 28–36). The female parent *E. chiapasana* has a dense covering of hairs and lacks lamellae and epicuticular wax. The male parent *E. berteroana* lacks hair but possesses lamellae and wax. The F_1 hybrid has scattered hairs, lamellae reduced in stature, and epicuticular wax.

In the interspecific hybridization that produced *Erythrina lysistemon* × *E. speciosa*, the male parent possesses two-armed hairs, which are lacking in the female parent; hairs are present in the F_1 hybrid, but again, at a rather lower density than in the male parent (Figs. 70–75).

These results demonstrate that it is possible to confirm hybridity in the progeny by examination of leaf epidermal characters. Many of the hybrids possess characters present in the male parent but absent in the female parent. There is no evidence

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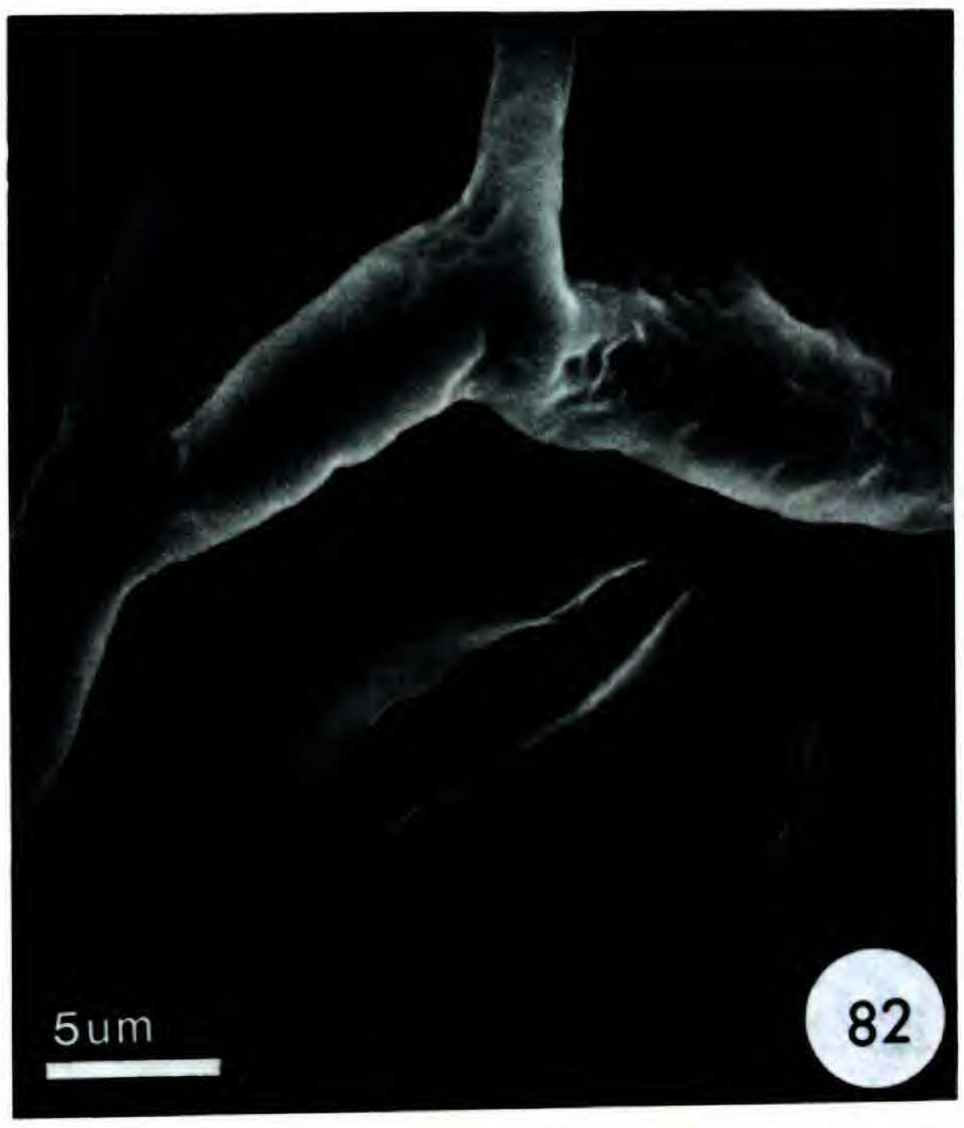
FIGURES 82–87. *SEM images, abaxial leaf surfaces of* E. crista-galli × E. guatemalensis *and parents. All photos at equal magnification.—82.* E. crista-galli, *WA 74p840, female parent.—83.* E. guatemalensis, *WA 74c1453, male parent.—84–87.* E. crista-galli × E. guatemalensis, *four F_1 siblings, PT 820548 and WA 82.278.*

FIGURES 88–93. *SEM images, abaxial leaf surfaces of* Erythrina crista-galli × E. fusca *and parents, and* E. dominguezii. *All photos at equal magnification.—88.* E. crista-galli, *WA 74p840, female parent.—89.* E. fusca, *WA 74s99, male parent.—90–92.* E. crista-galli × E. fusca, *three F_1 siblings, PT 840231 and HO 84.235.—93.* E. dominguezii, *PT 740234001.*

FIGURES 94–99. *SEM images, abaxial leaf surfaces of* Erythrina crista-galli × E. fusca *and parents, and* E. dominguezii. *All photos at equal magnification.—94.* E. crista-galli, *WA 74p840, female parent.—95.* E. fusca, *WA 74s99, male parent.—96–98.* E. crista-galli × E. fusca, *three F_1 siblings, PT 840231 and HO 84.235.—99.* E. dominguezii, *PT 740234001.*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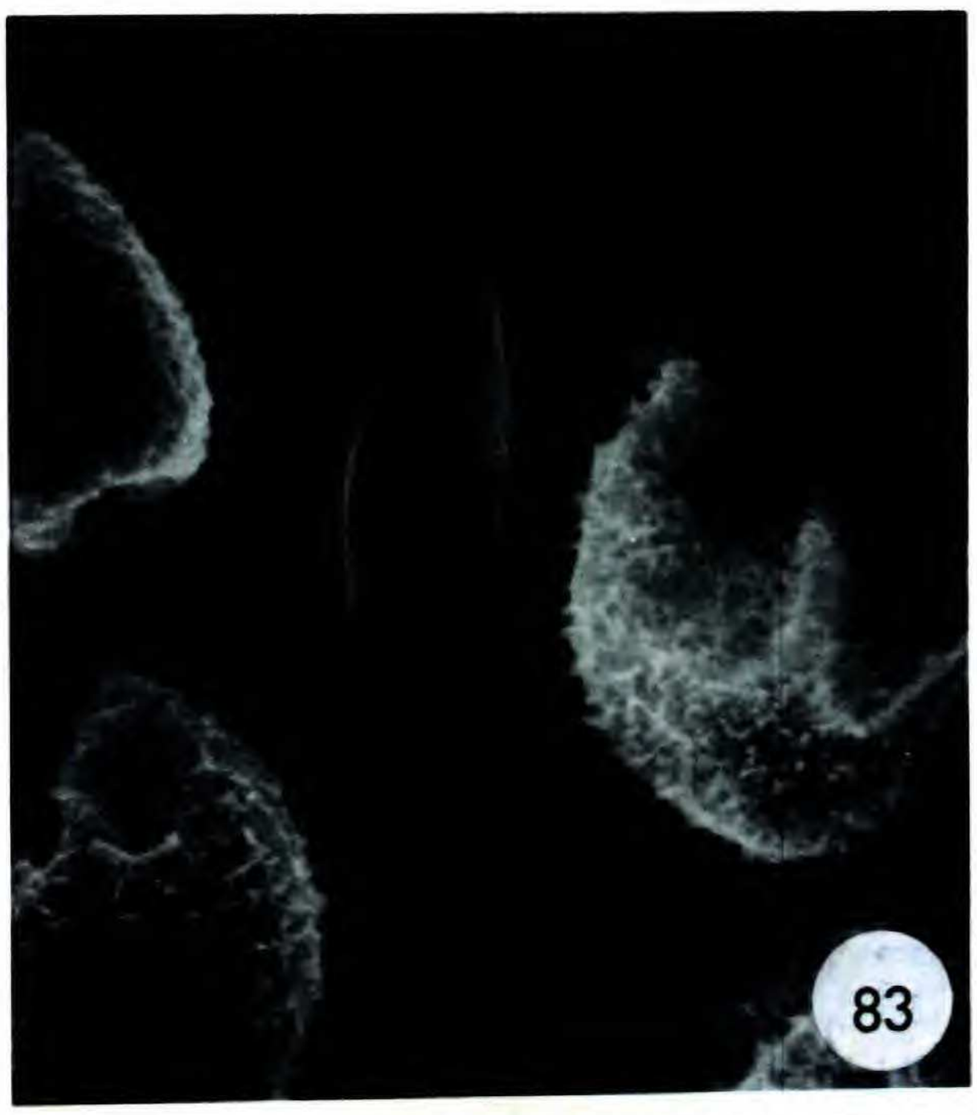
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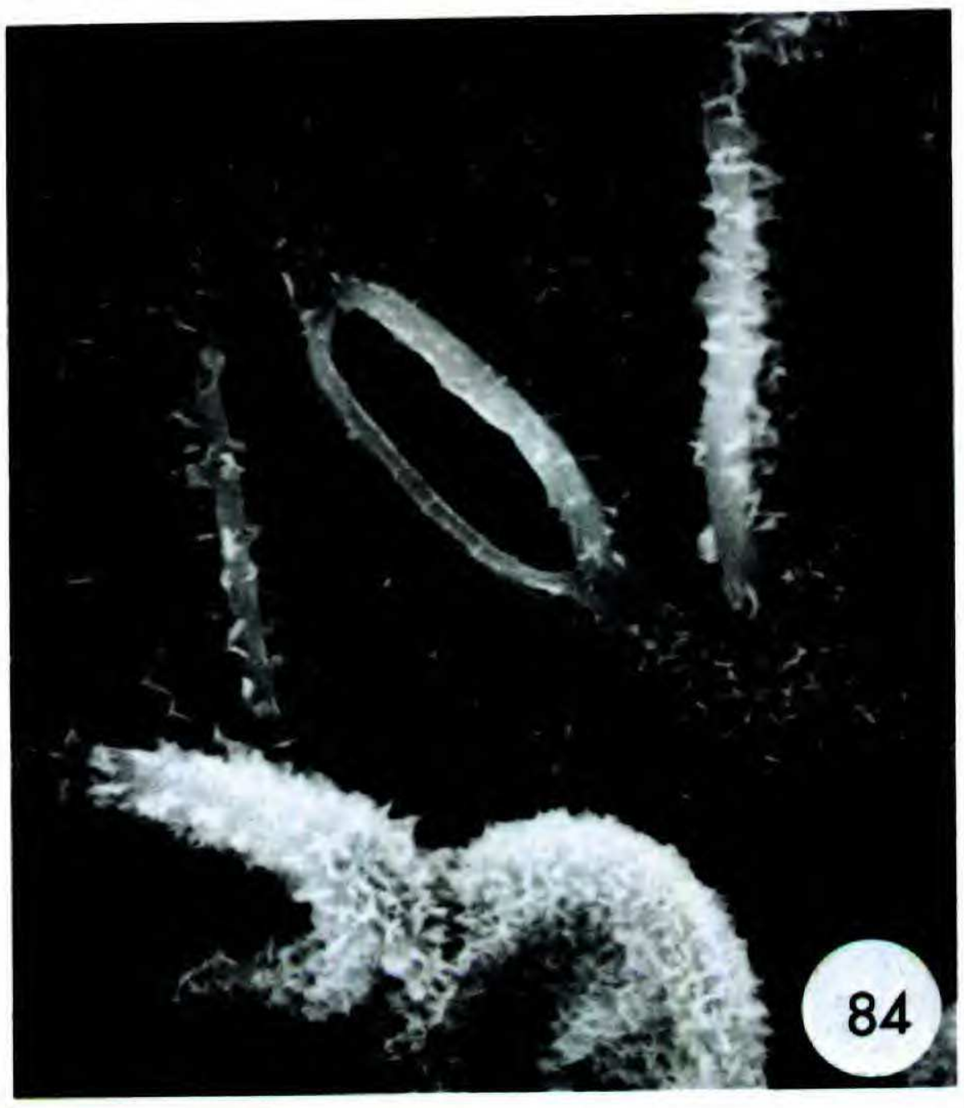
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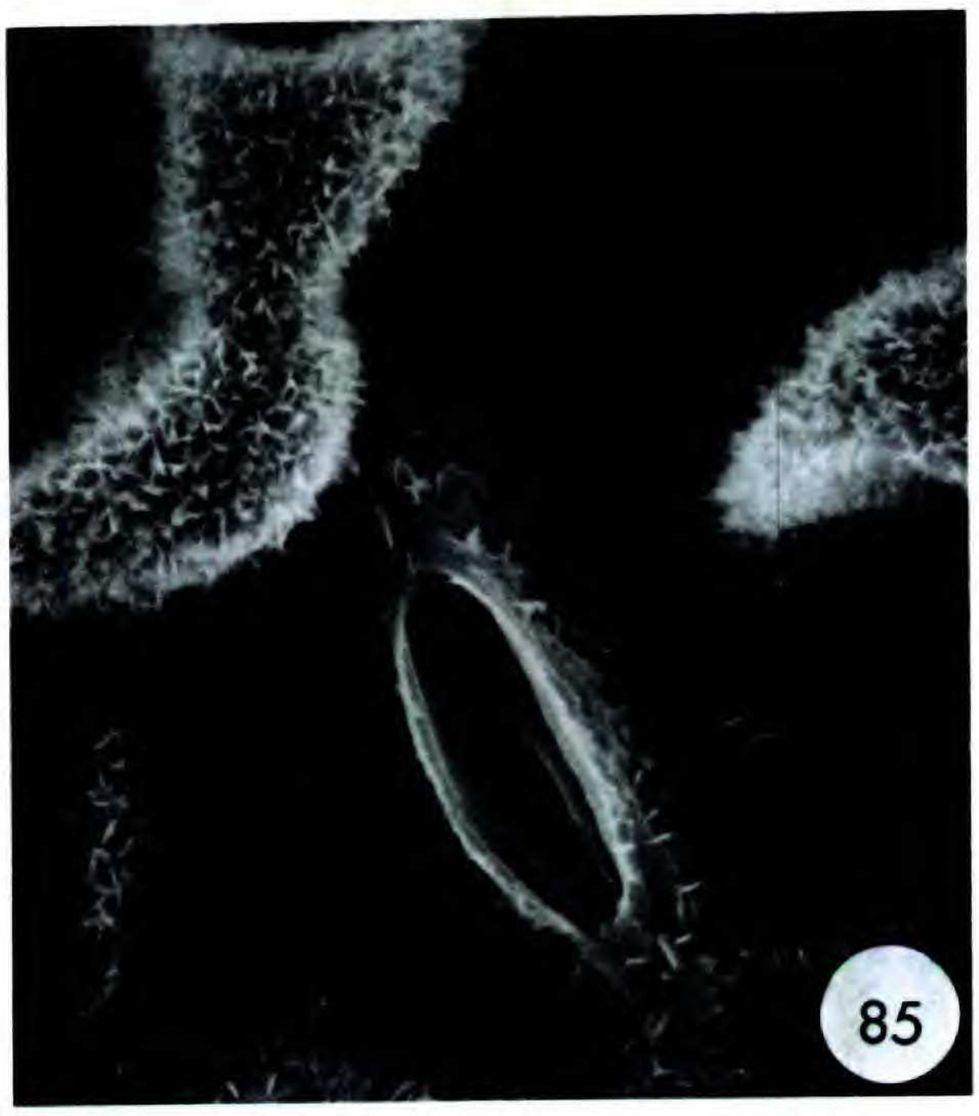
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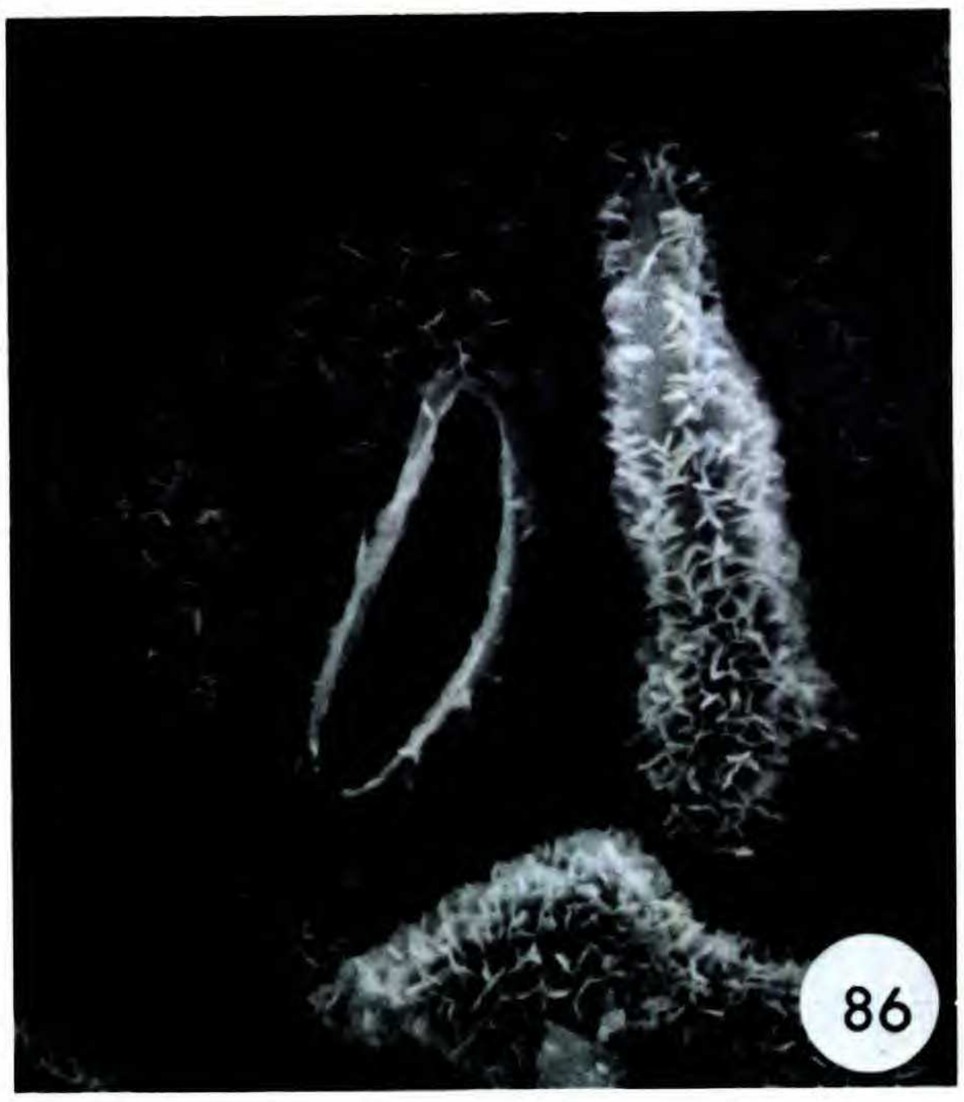
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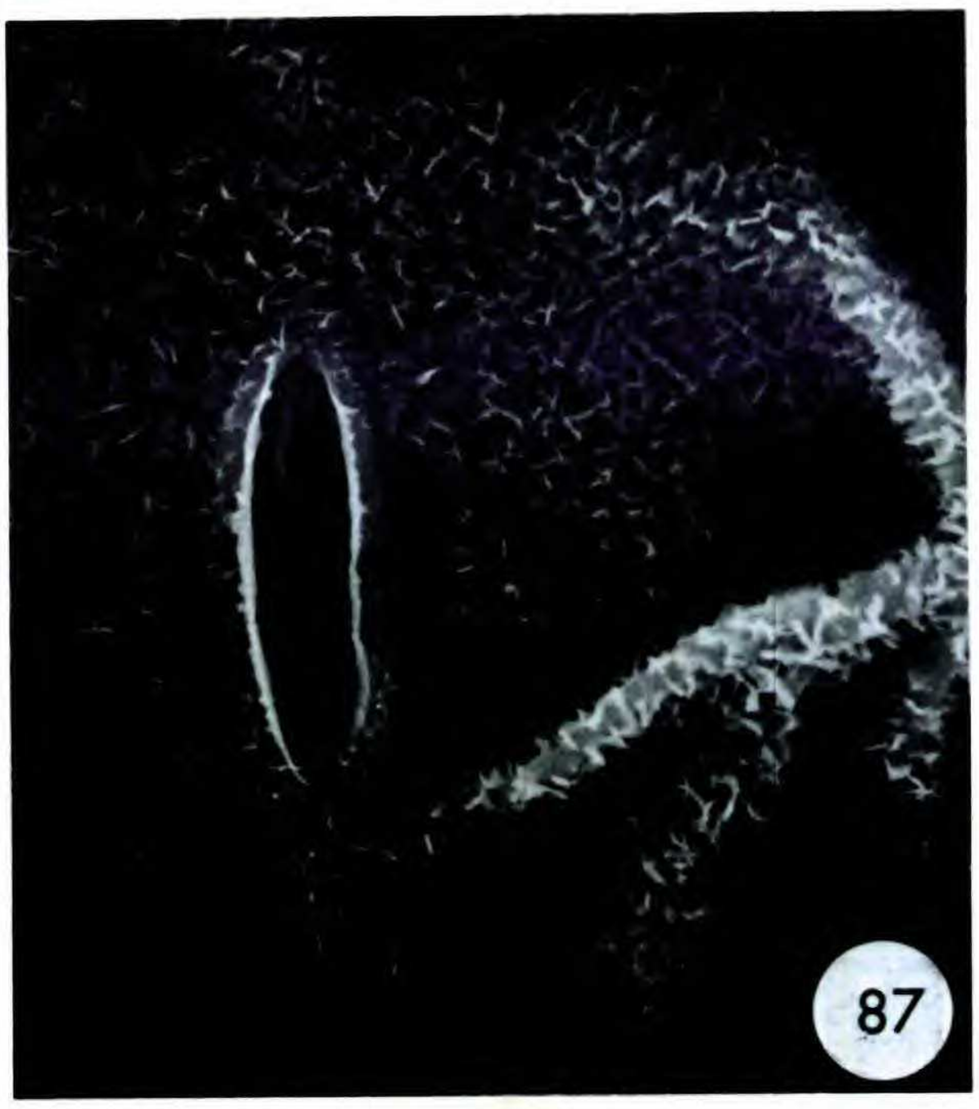
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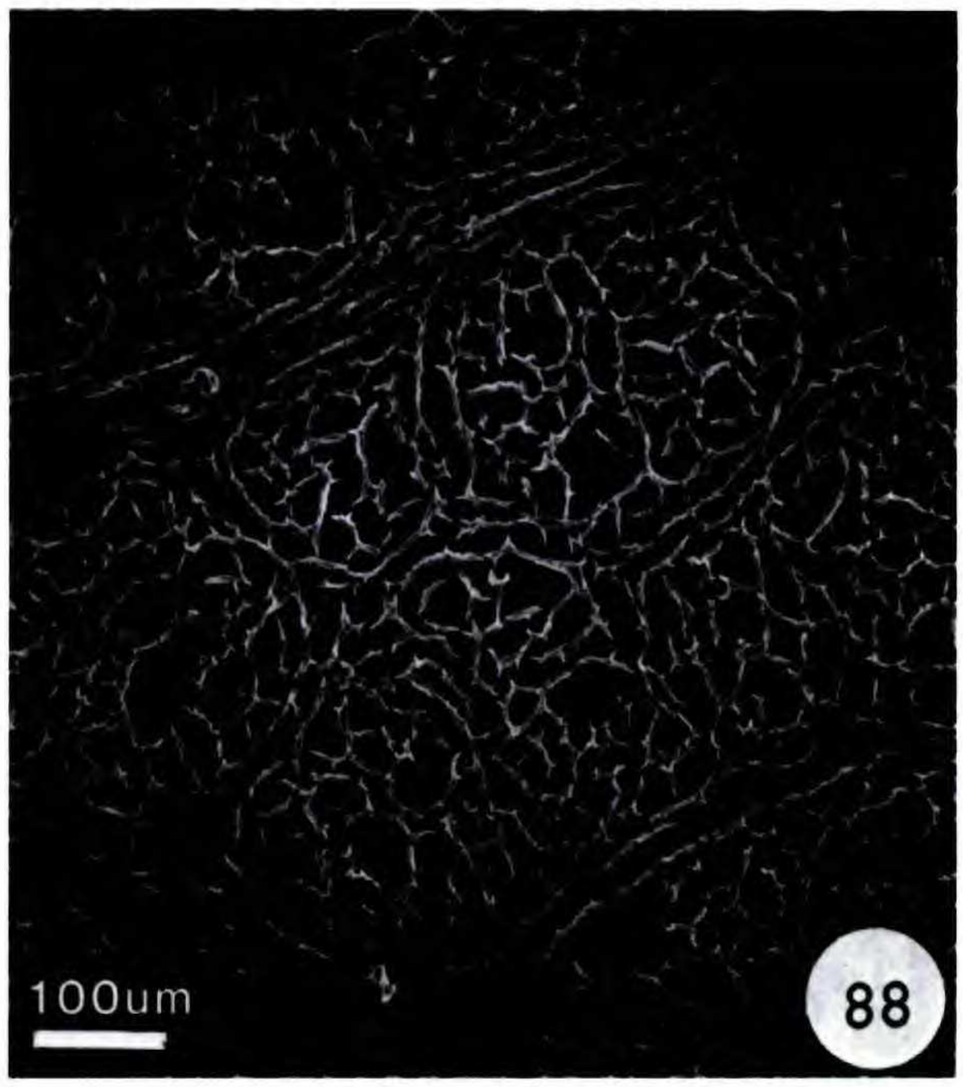
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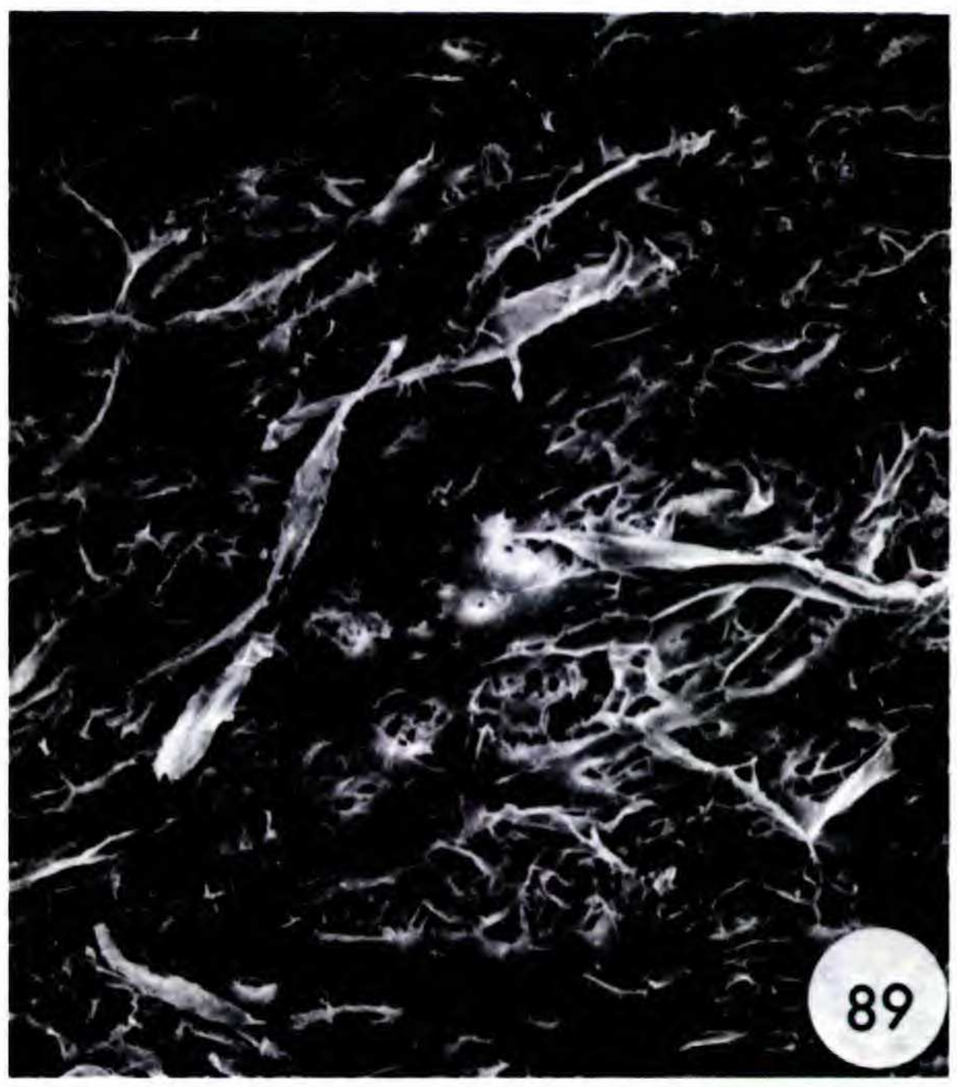
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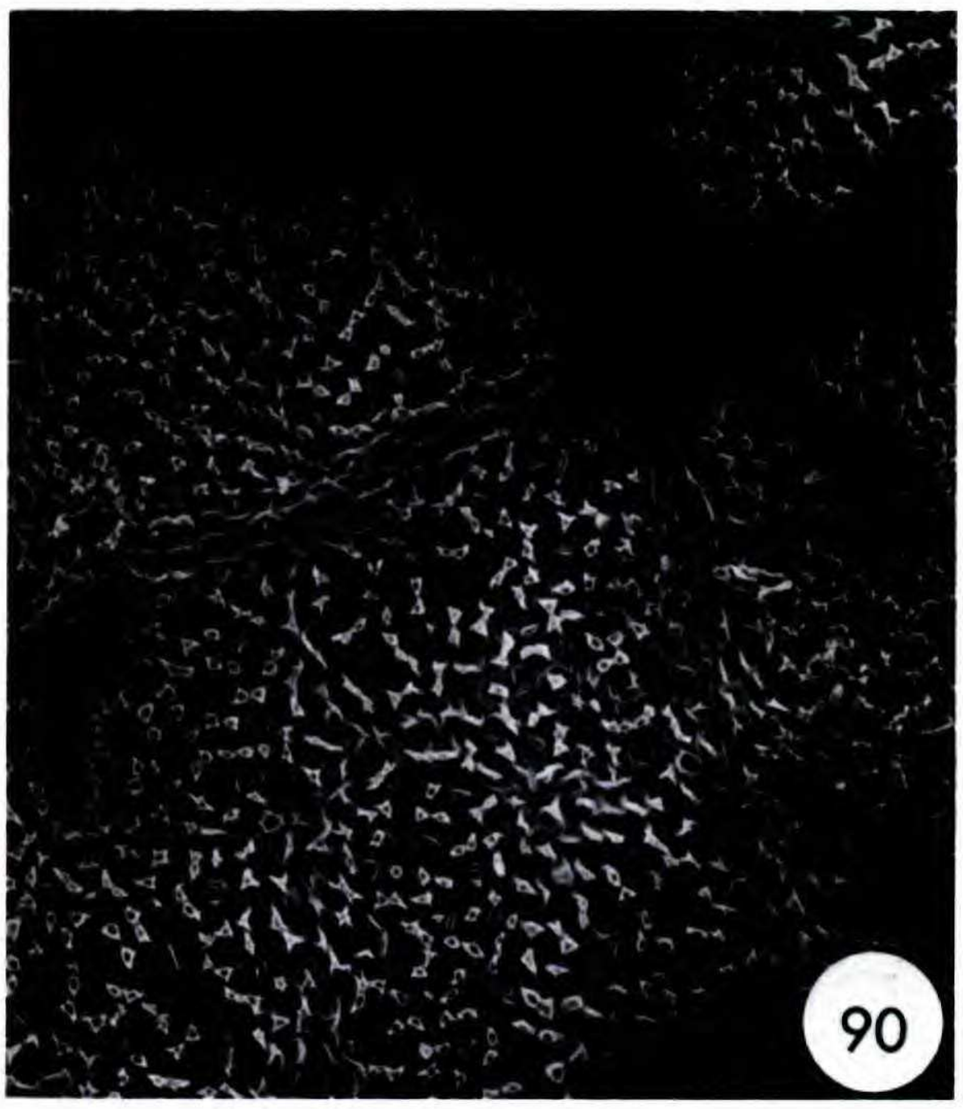
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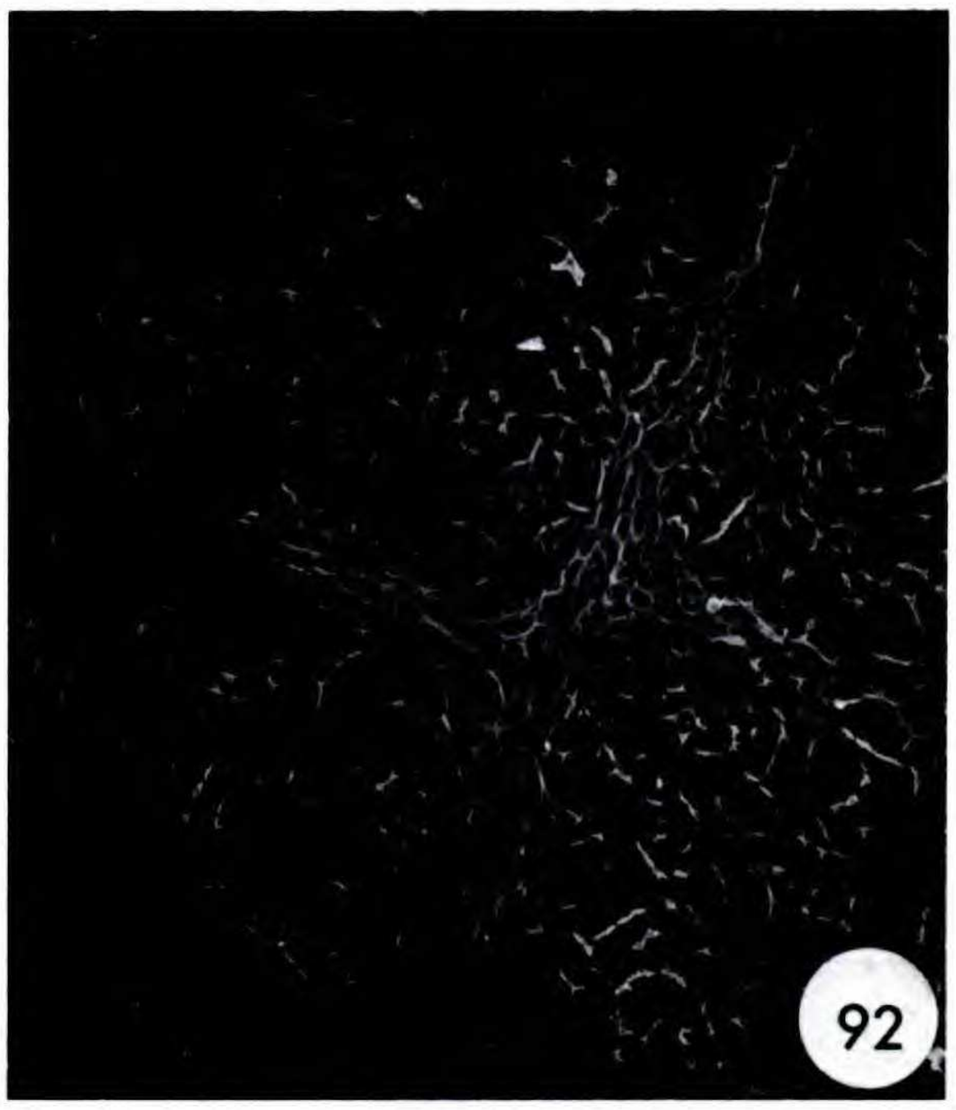
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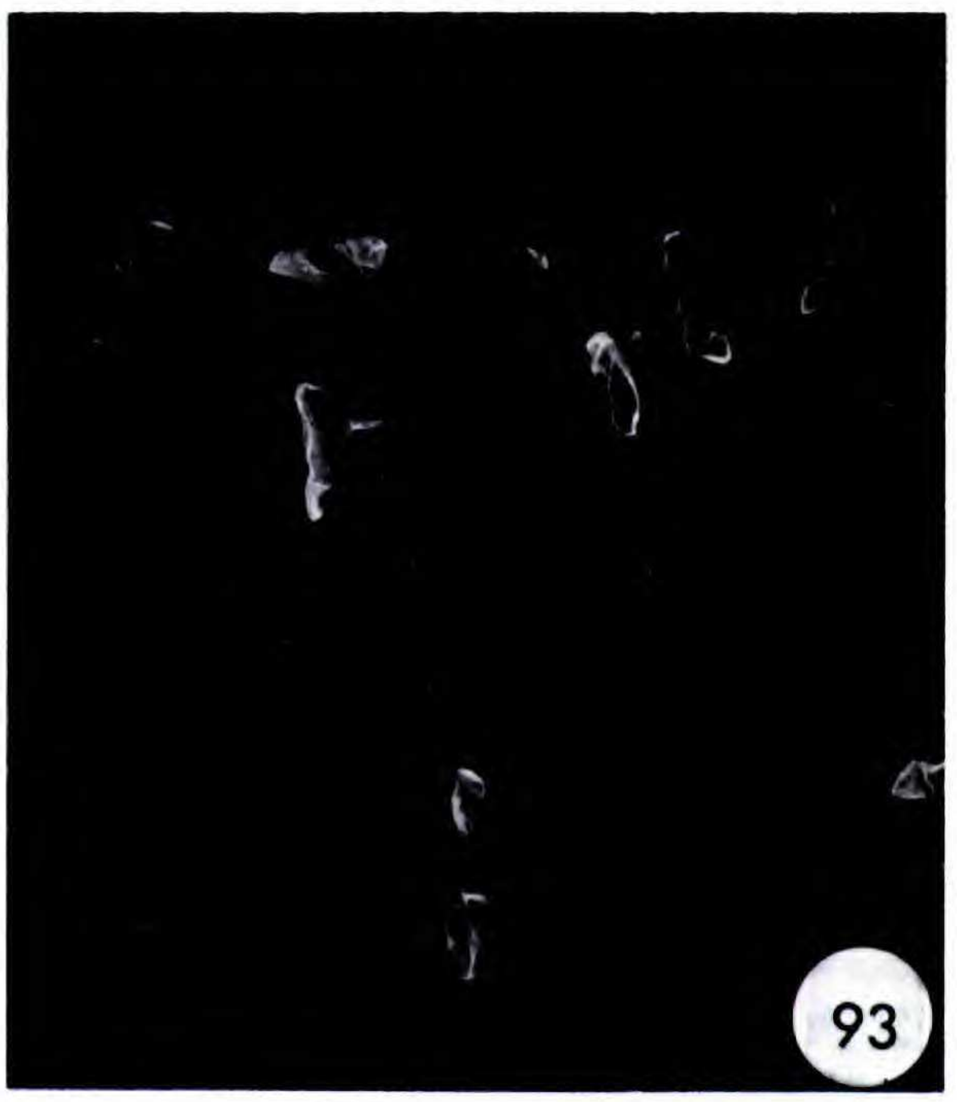
92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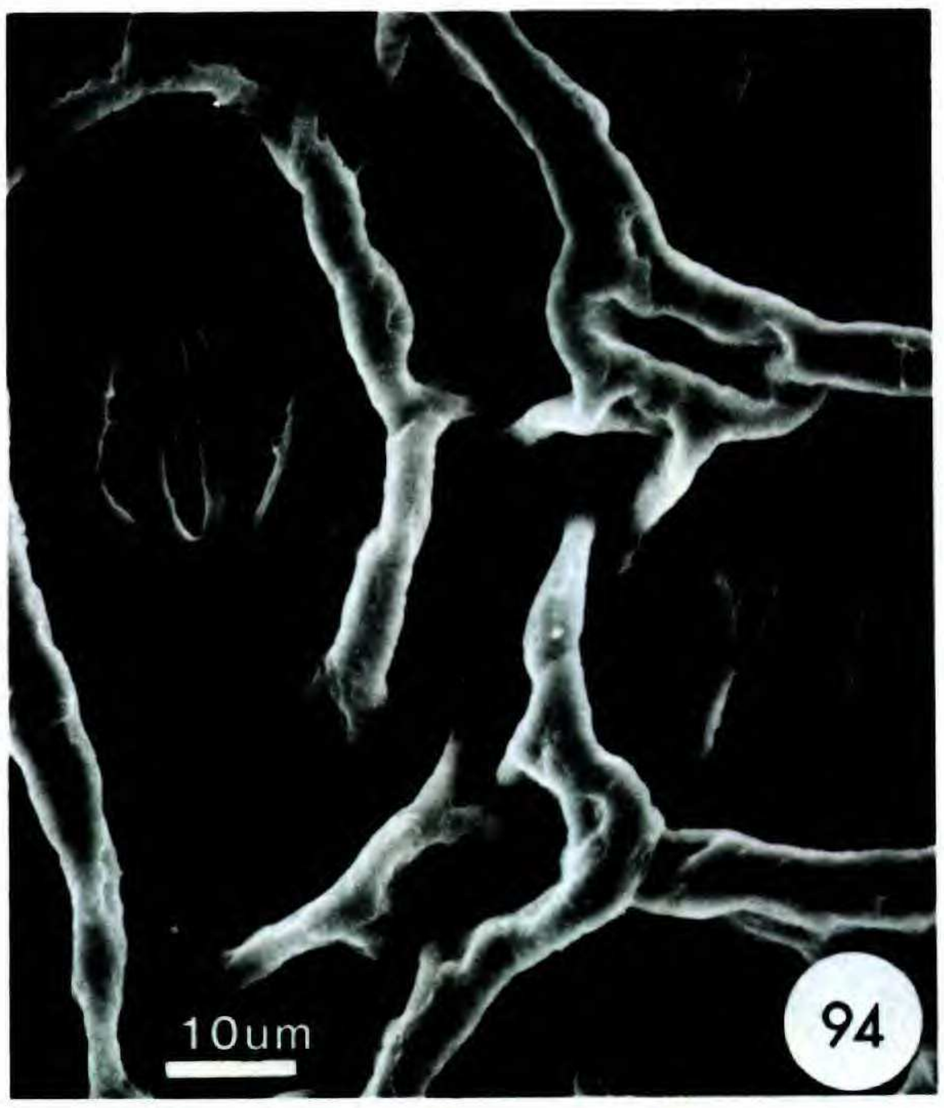
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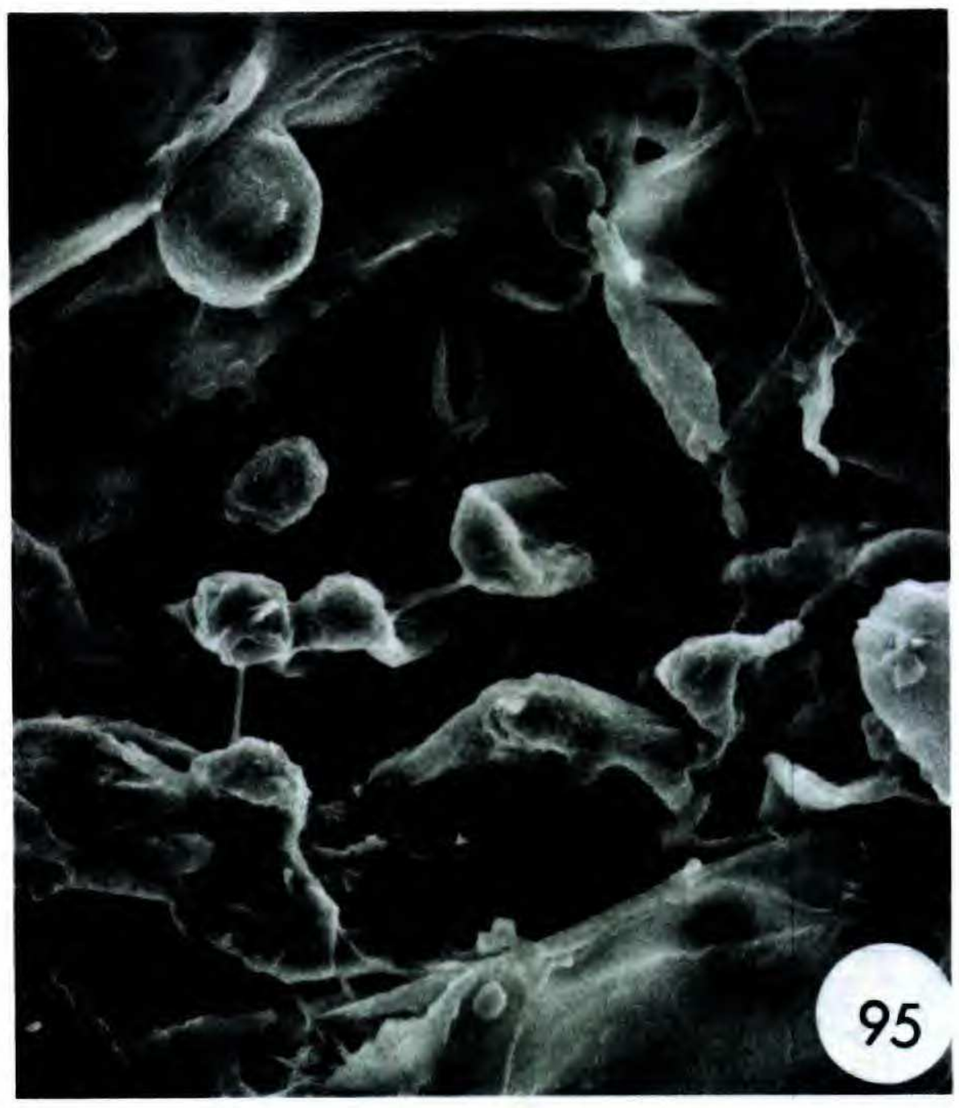
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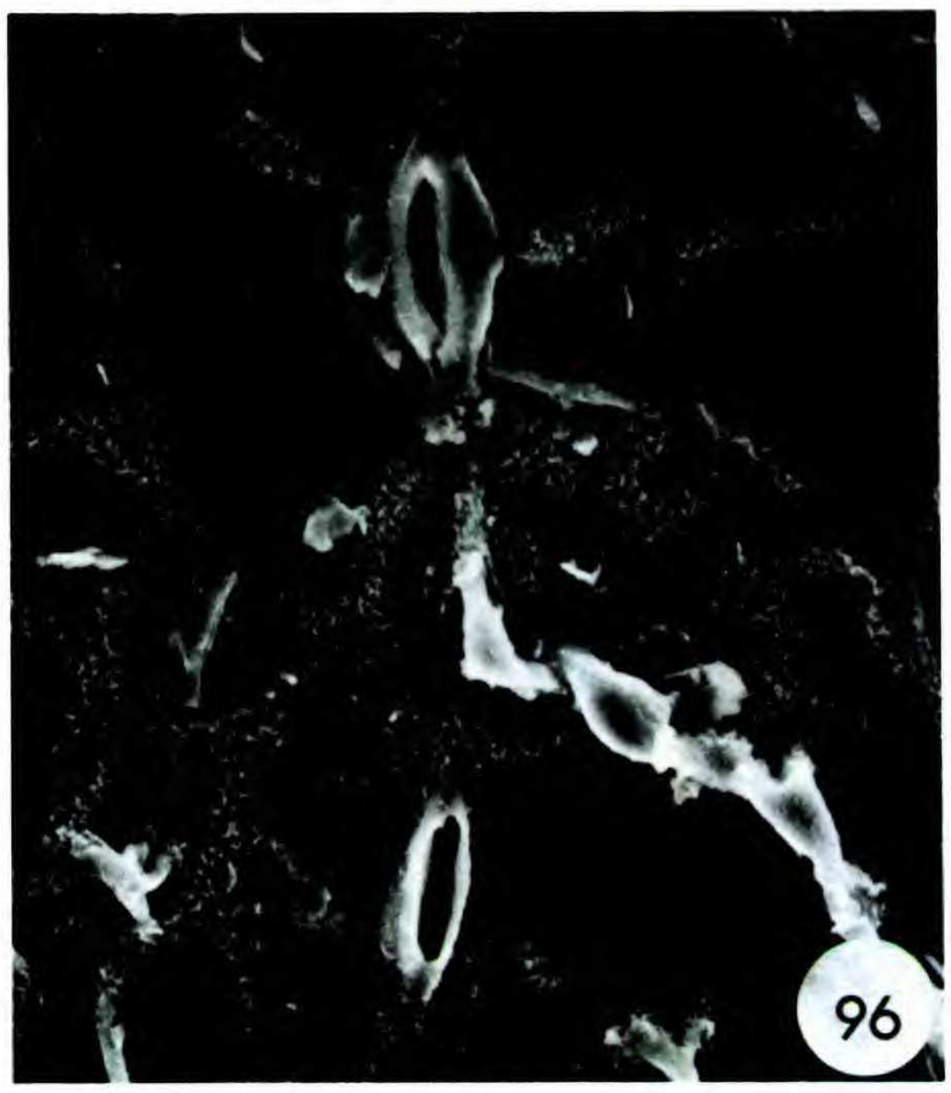
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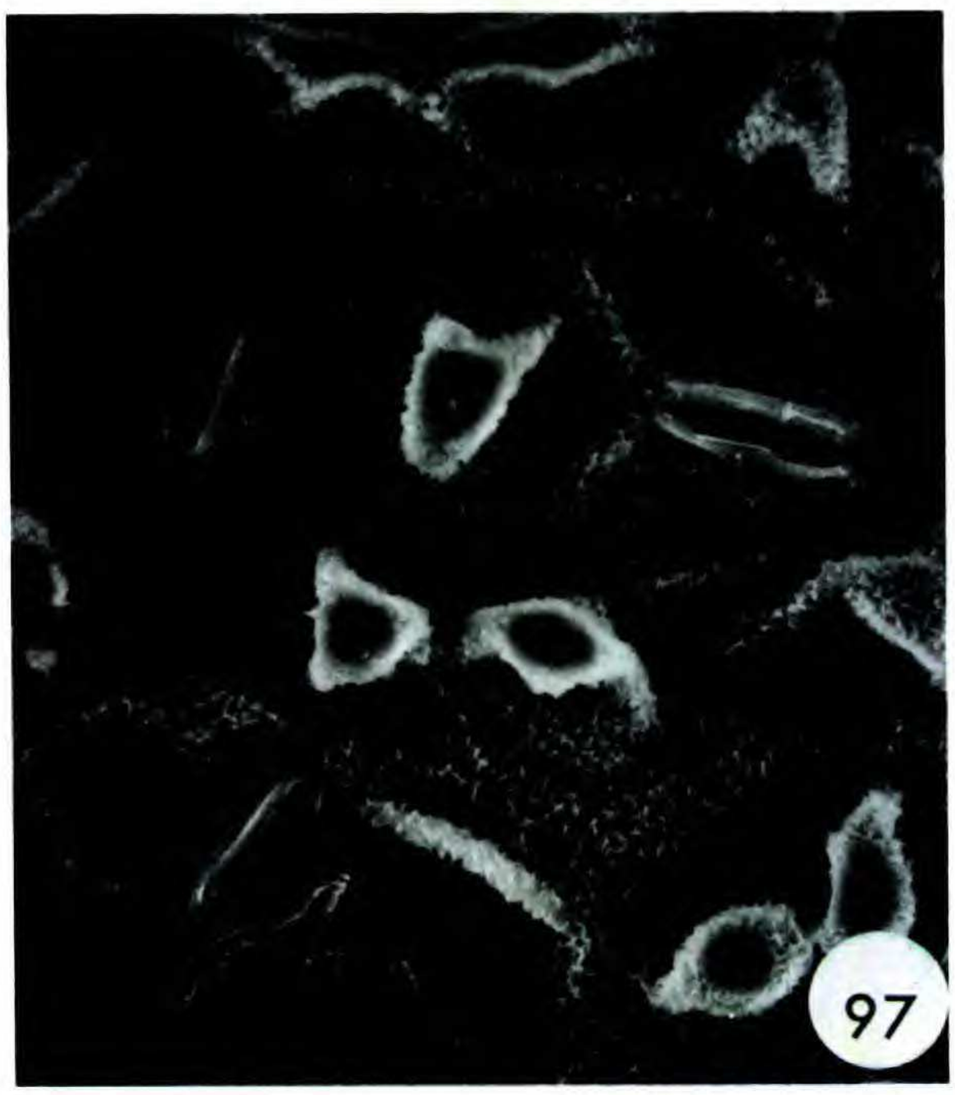
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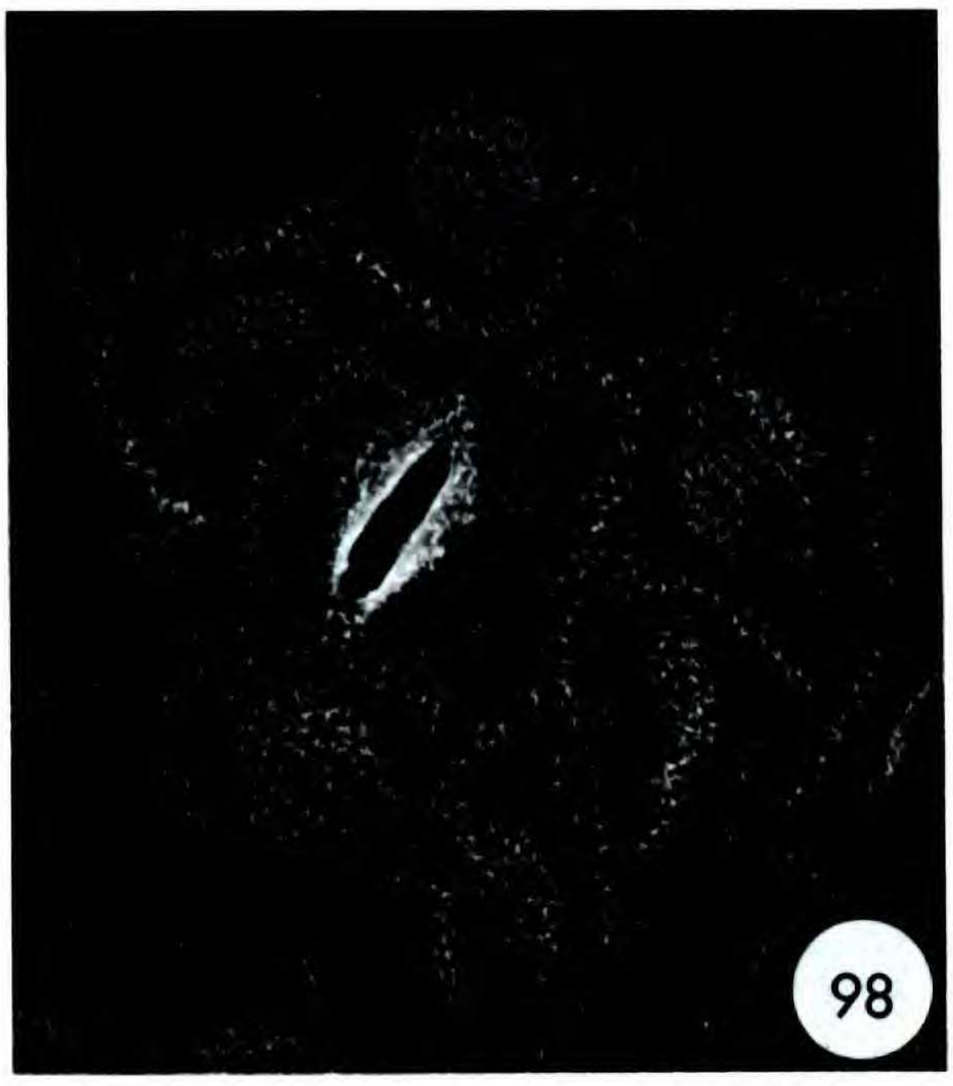
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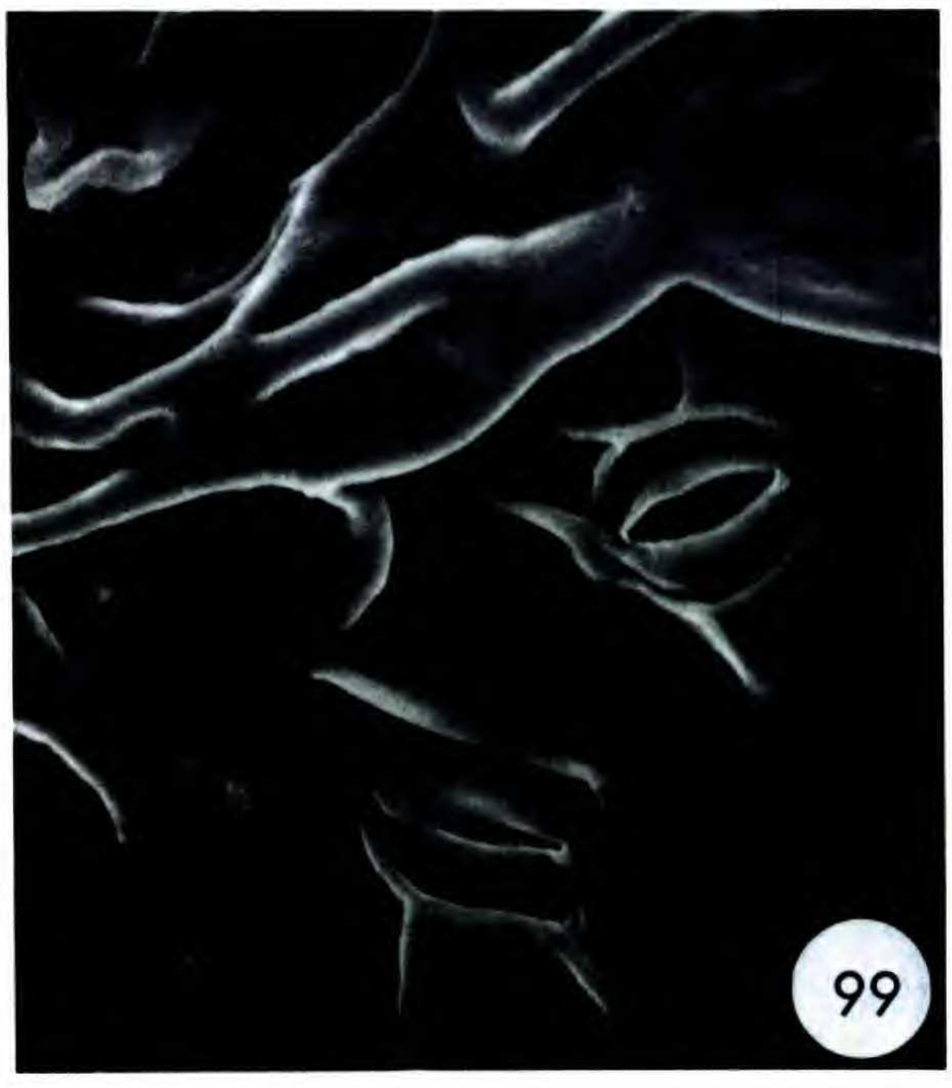
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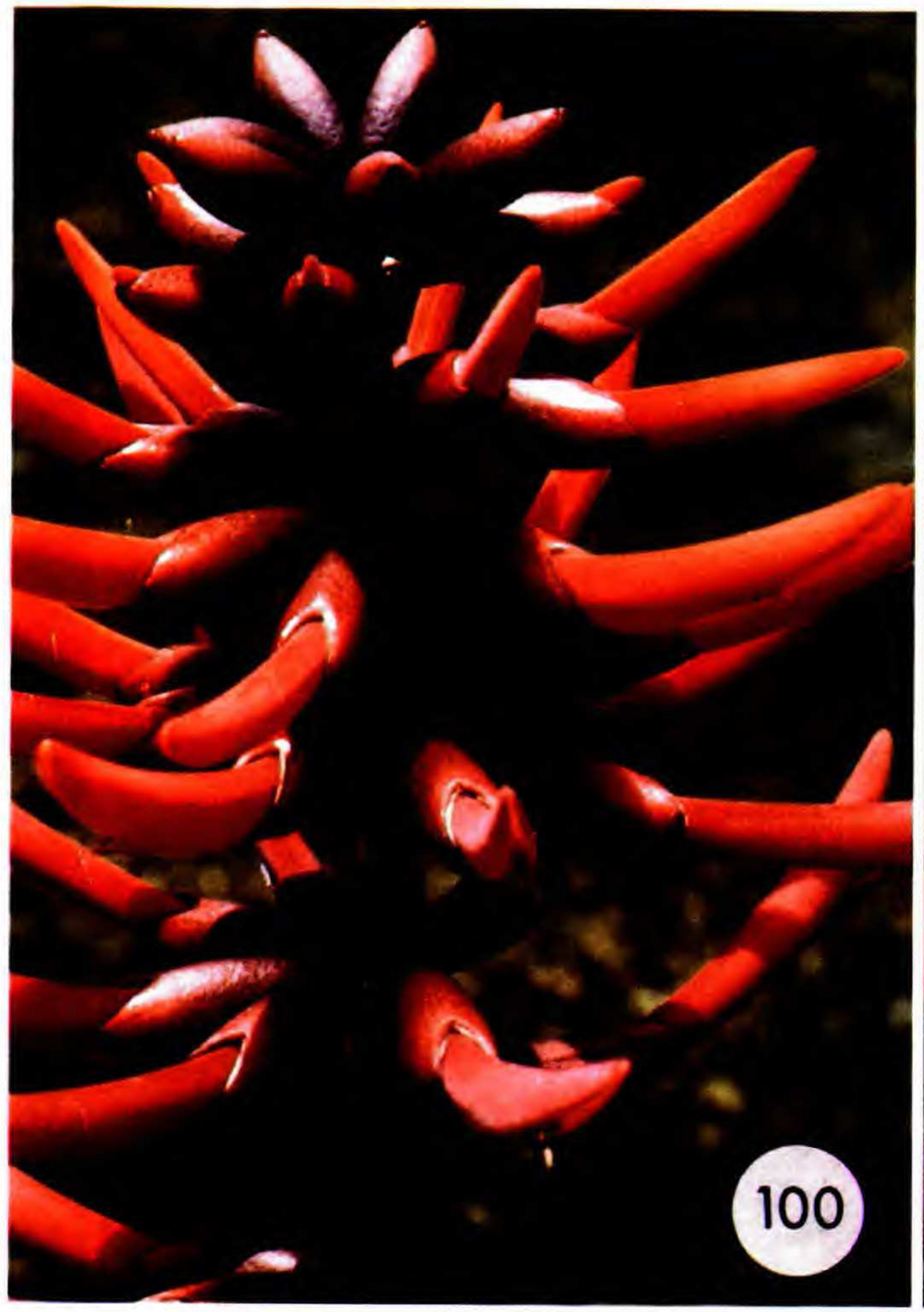
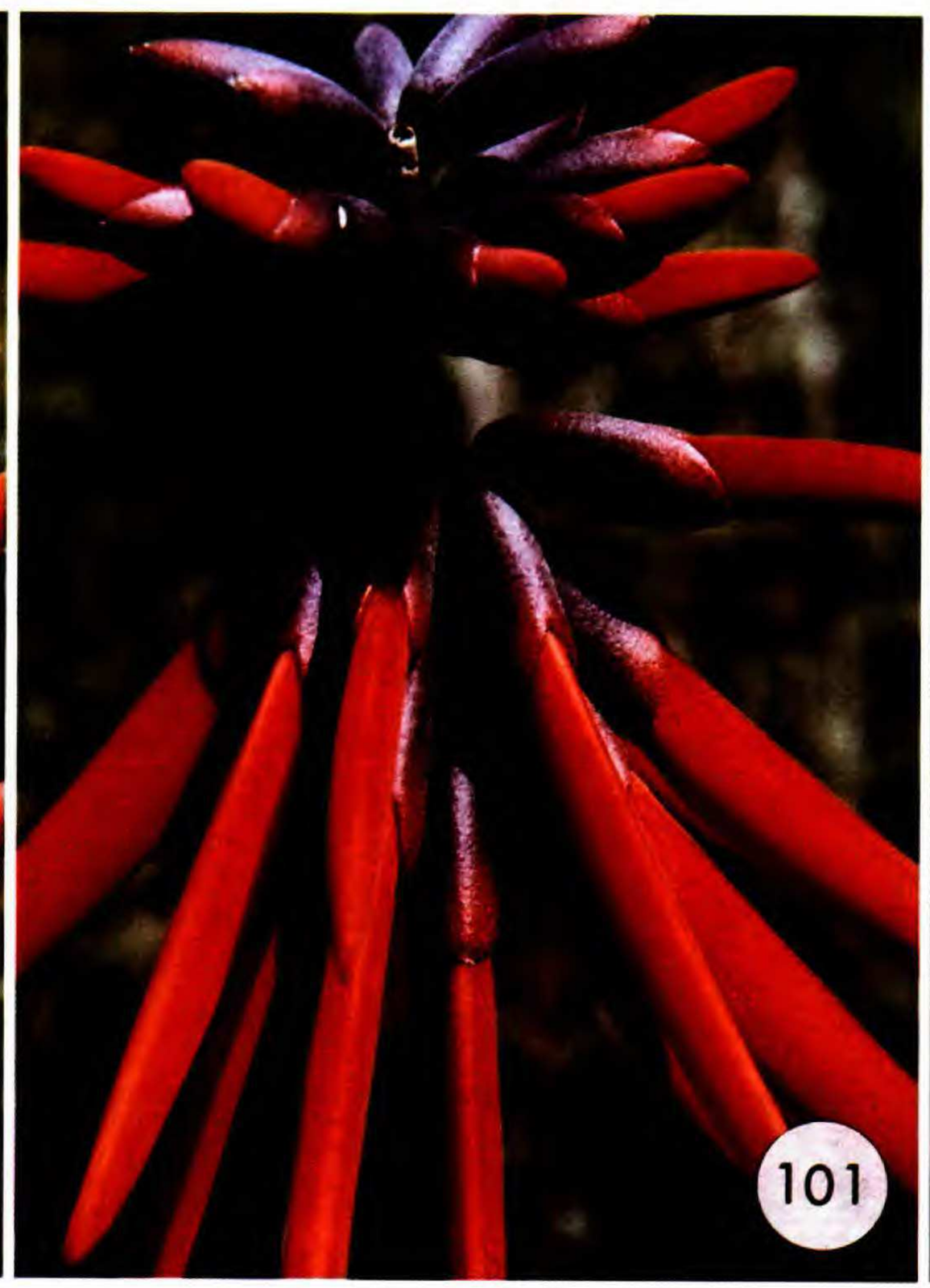
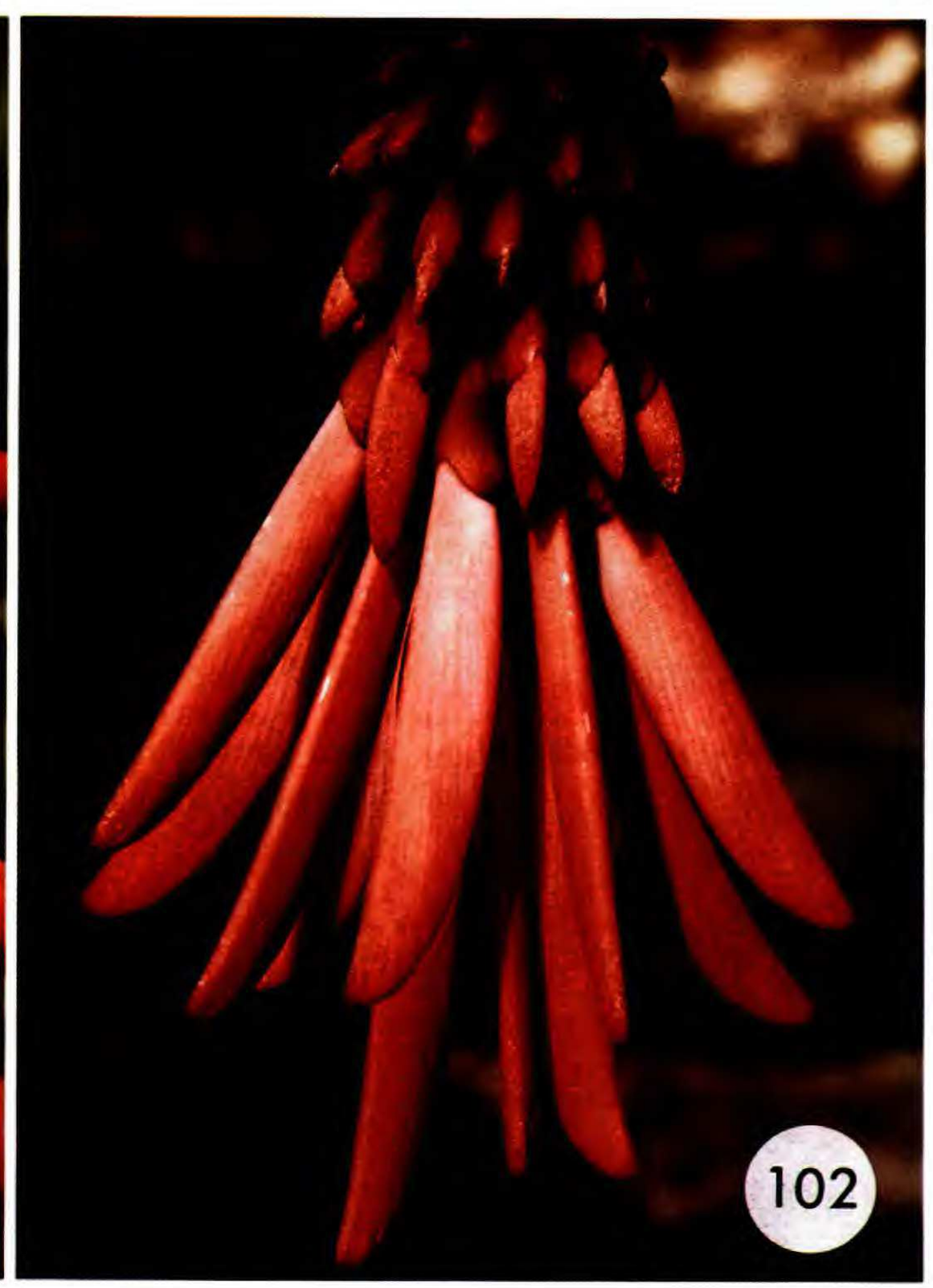






FIGURES 100–102. *Inflorescences of* Erythrina guatemalensis × E. folkersii *and parents.—100.* E. guatemalensis, *PT 700018001, female parent.—101.* E. guatemalensis × E. folkersii, *HO 82.282.—102.* E. folkersii, *PT 700010001, male parent.*

TABLE 19. *Comparison of flowers of F_1 hybrids and their parents in sect.* Erythrina. *Color code in "Standard Color" refers to Berlin & Kay color chart; see Croat (1983).*

	Female Parent	F_1 Hybrid	Male Parent
Figure 103	*E. berteroana* WA 78s564	HO 82.647	*E. guatemalensis* WA 74c1453
CALYX			
Shape	oblong	oblong to elliptic	elliptic
Apex shape	oblique; longer on carinal side	oblique; longer on carinal side	irregular; bilabiate or oblique
Length (cm)			
Vexillar side	2.2–2.3	2.2–2.4	2.3–2.7
Carinal side	2.6–2.7	2.7–2.8	2.6–2.9
Width (cm)			
Greatest	0.8	1.0–1.1	1.2–1.3
Middle	0.8	1.0–1.1	1.2–1.3
Indumentum	glabrous	sparsely puberulent	glabrous
Texture	smooth	minutely papillate	minutely papillate
Color	pale red	red to reddish brown	reddish brown
COROLLA			
Standard			
Color	red 8/7.5	red 8/7.5	red 6/7.5
Length (cm)	8.7	7.5	6.5
Greatest width (cm)	1.6	1.6	1.8
Wings			
Shape	apex acute	apex acute to rounded	apex rounded
Length (cm)	1.2	1.1	1.3
Width (cm)	0.3	0.4	0.3
Keel			
Shape	emarginate; each half acute at apex	apex short-apiculate	apex rounded
Length (cm)	1.0	1.1	1.3
Width (cm)	0.8	1.0	1.0

	E. guatemalensis		*E. tajumulcensis*
Figure 104	WA 74c1453	PT 820547001	WA 74c1448
CALYX			
Shape	elliptic	oblong	oblong
Apex shape	variable; bilabiate or oblique	oblique; longer on carinal side	oblique; longer on carinal side
Length (cm)			
Vexillar side	2.3–2.7	2.3–2.5	2.4–2.6
Carinal side	2.6–2.9	2.7–2.8	2.7–3.0
Width (cm)			
Greatest	1.2–1.3	0.9	0.7
Middle	1.2–1.3	0.9	0.7
Indumentum	glabrous	glabrous	glabrous
Texture	minutely papillate	smooth	smooth
Color	reddish brown		red
COROLLA			
Standard	red 6/7.5	red 7/7.5	red 6/7.5
Color	6.5	7.2	9.3
Length (cm)	1.8	1.5	1.3
Greatest width (cm)			

TABLE 19. *Continued.*

	Female Parent	F_1 Hybrid	Male Parent
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong, apex rounded
Length (cm)	1.3	1.0	1.0
Width (cm)	0.4	0.4	0.3
Keel			
Shape	apex rounded	emarginate; each half short-apiculate at apex	apex long-acuminate
Length (cm)	1.3	1.1	1.3
Width (cm)	1.0	1.8	1.0

Figure 105	*E. guatemalensis* PT 700018001	HO 82.282	*E. folkersii* PT 700010001
CALYX			
Shape	elliptic; broadest in middle	cuneate; broadest at apex	cuneate; broadest at apex
Apex shape	irregular; oblique or bilabiate	oblique to truncate	oblique; longer on side
Length (cm)			
Vexillar side	2.3–2.7	1.8–1.9	1.8–1.9
Carinal side	2.6–2.9	2.2–2.5	2.1–2.2
Width (cm)			
Greatest	1.2–1.3	1.2–1.3	1.2
Middle	1.2–1.3	1.0	0.8
Indumentum	glabrous	sparsely puberulent	densely puberulent
Texture	minutely papillate	minutely papillate	minutely papillate
Color	reddish brown	reddish brown to purple-brown	light brown
COROLLA			
Standard			
Color	red 6/7.5	red 6/10	red 7/7.5
Length (cm)	6.5	7.0–7.8	8.0
Greatest width (cm)	1.8	2.2	2.4
Wings			
Shape	apex rounded	apex rounded	apex rounded
Length (cm)	1.3	1.1–1.3	1.0
Width (cm)	0.4	0.5	0.5
Keel			
Shape	apex rounded	apex variable; rounded or emarginate	emarginate, each half obtuse at apex
Length (cm)	1.3	1.2–1.3	1.0
Width (cm)	1.0	0.9	1.3

Figure 106	*E. guatemalensis* PT 700018001	HO 82.284 PT 820278002 (2 individuals)	*E. chiapasana* PT 73071001
CALYX			
Shape	elliptic	oblong to elliptic	oblong
Apex shape	variable; bilabiate or oblique	truncate to oblique; 5 apical lobes in bud, absent in anthesis	truncate; 5 apical lobes in bud, absent at anthesis
Length (cm)			
Vexillar side	2.3–2.7	1.7–1.9	1.5–1.6
Carinal side	2.6–2.9	1.7–2.1	1.5–1.6

TABLE 19. *Continued.*

	Female Parent	F_1 Hybrid	Male Parent
Width (cm)			
Greatest	1.2–1.3	0.9	0.8
Middle	1.2–1.3	0.8–0.9	0.7
Indumentum	glabrous	sparsely puberulent	densely puberulent
Texture	minutely papillate	smooth	smooth to indistinctly 5-angled
Color	reddish brown	reddish brown to green	green
COROLLA			
Standard			
Color	red 6/7.5	red 5/5 to 5/7.5	red 5/7.5
Length (cm)	6.5	6.5	7.4
Greatest width (cm)	1.8	1.5–1.8	1.4
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.5	1.3–1.4
Width (cm)	0.4	0.4	0.4
Keel			
Shape	apex rounded	variable; apex rounded or emarginate	emarginate; each half short-apiculate
Length (cm)	1.3	1.0–1.3	1.3
Width (cm)	1.0	0.9–1.0	0.9
Figure 107	*E. guatemalensis* PT 700018001	HO 82.285 HO 82.288 PT 820276001	*E. macrophylla* PT 750420002
CALYX			
Shape	elliptic; broadest in middle	oblong to elliptic	cuneate; broadest at apex
Apex shape	variable; bilabiate or oblique	truncate to slightly oblique; 5 irregular apical lobes	truncate; 5 prominent, blunt lobes
Length (cm)			
Vexillar side	2.3–2.7	1.8–2.5	2.0
Carinal side	2.6–2.9	2.3–2.6	2.0
Width (cm)			
Greatest	1.2–1.3	1.0–1.2	1.2 (at apex)
Middle	1.2–1.3	1.0–1.2	0.9
Indumentum	glabrous	sparsely to densely puberulent	densely puberulent
Texture	minutely papillate	obscurely 5-angled	longitudinally 5-angled
Color	reddish brown	reddish brown to green	brown to green
COROLLA			
Standard			
Color	red 6/7.5	red 6/7.5 to 6/10	red 5/7.5
Length (cm)	6.5	6.4–7.0	6.4
Greatest width (cm)	1.8	1.7–2.1	1.7
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.3–1.6	1.3
Width (cm)	0.4	0.4–0.5	0.4
Keel			
Shape	apex rounded	apex short-apiculate	apex short-apiculate
Length (cm)	1.3	1.1–1.3	1.3
Width (cm)	1.0	1.1–1.2	1.1

TABLE 19. *Continued.*

	Female Parent	F_1 Hybrid	Male Parent
Figure 108	*E. macrophylla* PT 750420002	HO 82.763 (2 individuals)	*E. guatemalensis* PT 700018001
CALYX			
Shape	cuneate; broadest at apex	elliptic	elliptic; bilabiate in middle
Apex shape	truncate; 5 prominent apical lobes	variable; bilabiate or truncate; 5 indistinct apical lobes present or lacking	variable; bilabiate or oblique
Length (cm)			
Vexillar side	2.0	1.9–2.2	2.3–2.7
Carinal side	2.0	2.0–2.4	2.6–2.9
Width (cm)			
Greatest	1.2 (at apex)	1.1–1.2	1.2–1.3
Middle	0.9	1.1–1.2	1.2–1.3
Indumentum	densely puberulent	densely puberulent	glabrous
Texture	longitudinally 5-angled	smooth to minutely papillate	minutely papillate
Color	brown to green	reddish brown to green	reddish brown
COROLLA			
Standard			
Color	red 5/7.5	red 5/7.5	red 6/7.5
Length (cm)	6.4	6.5–6.7	6.5
Greatest width (cm)	1.7	1.8	1.8
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.3	1.3
Width (cm)	0.4	0.4–0.5	0.4
Keel			
Shape	apex short-apiculate	apex rouuded	apex rounded
Length (cm)	1.3	1.0–1.1	1.3
Width (cm)	1.1	1.1–1.2	1.0
Figure 109	*E. chiapasana* PT 721005001	HO 82.278 (2 individuals)	*E. beteroana* PT 700044002
CALYX			
Shape	oblong	oblong	oblong
Apex shape	truncate; 5 indistinct apical knobs	truncate	oblique; longer on carinal side
Length (cm)			
Vexillar side	1.5–1.6	2.2–2.3	2.8
Carinal side	1.5–1.6	2.2–2.4	3.0
Width (cm)			
Greatest	0.8	0.9	0.8
Middle	0.7	0.8–0.9	0.7
Indumentum			
Texture	indistinct longitudinal ridges	indistinct longitudinal ridges	smooth
Color	green	pale green to red	pale red
COROLLA			
Standard			
Color	red 5/7.5	red 6/5 to 8/7.5	red 8/7.5 to 9/7.5
Length (cm)	6.8	8.5	8.3
Greatest width (cm)	1.4	1.6–1.7	1.6

TABLE 19. *Continued.*

	Female Parent	F_1 Hybrid	Male Parent
Wings			
Shape	oblong; apex rounded	oblong; apex acute to rounded	oblong; apex acute
Length (cm)	1.5	1.2	1.0
Width (cm)	0.4	0.4	0.4
Keel			
Shape	emarginate, each half short apiculate	apex rounded to emarginate	deeply emarginate; each half acute at apex
Length (cm)	1.3	1.0	0.8
Width (cm)	0.9	0.9	0.9
Figure 110	*E. macrophylla* PT 750420002	HO 82.281 (2 individuals)	*E. beteroana* PT 700044001
CALYX			
Shape	cuneate; broadest at apex	oblong	oblong, narrow
Apex shape	truncate; 5 prominent apical lobes	truncate; 5 indistinct apical lobes	oblique; longer on carinal side
Length (cm)			
Vexillar side	2.0	2.2–2.4	2.8
Carinal side	2.0	2.2–2.4	3.0
Width (cm)			
Greatest	1.2	1.0–1.1	0.7
Middle	0.9	0.7–0.8	0.7
Indumentum	densely puberulent	sparsely puberulent	glabrous
Texture	longitudinally 5-angled	indistinct longitudinal ridges	smooth
Color	brown to green	green to red	pale red to green
COROLLA			
Standard			
Color	red 5/7.5	red 6/7.5	red 8/7.5
Length (cm)	6.4	7.3–7.4	8.3
Greatest width (cm)	1.7	1.5–1.6	1.3
Wings			
Shape	oblong; apex rounded	oblong; apex acute to rounded	oblong; apex acute
Length (cm)	1.3	1.0–1.2	1.0
Width (cm)	0.4	0.4	0.4
Keel			
Shape	apex short-apiculate	apex apiculate or emarginate	deeply emarginate; each half acute at apex
Length (cm)	1.3	1.0–1.1	0.8
Width (cm)	1.1	0.8–1.0	0.9

of matrocliny or female-dominant inheritance in the *Erythrina* hybrids.

The results, although preliminary, also suggest a difference in the genetics of inheritance of hairs on the one hand, and papillae and lamellae on the other. Hairs are inherited in the hybrids as discrete characters—that is, they are fully formed and of normal size, although they occur at low densities, in crosses between hairy and hairless parents. The formation of hairs may thus be controlled by a single gene or supergene, with modifiers controlling density of the hairs. On the other hand, in crosses between papillate (or lamellate) and nonpapillate parents, papillae (lamellae) may be present but they are much reduced in stature. This suggests that the stature of papillae and lamellae are continuously variable, typical of morphometric traits, and controlled by many genes, each of small effect.

TABLE 20. *Comparison of flowers of* Erythrina atitlanensis *and* F_1 *hybrid*, E. macrophylla × E. berteroana. *(Photo, Fig. 111.)*

	E. atitlanensis WA 74s98 WA 75s1141	*E. macrophylla* × *E. berteroana* HO 82.281
CALYX		
Shape	oblong	oblong
Apex shape	truncate; 5 indistinct apical lobes	truncate; 5 indistinct apical lobes
Length (cm)		
Vexillar side	1.7–1.8	2.2–2.4
Carinal side	1.8–1.9	2.2–2.4
Width (cm)		
Greatest	1.0	1.0–1.1
Middle	0.7	0.7–0.8
Indumentum	sparsely puberulent	sparsely puberulent
Texture	indistinct longitudinal ridges	indistinct longitudinal ridges
Color	pale green to red	green to red
COROLLA		
Standard		
Color	red 6/7.5	red 6/7.5 to 7/10
Length (cm)	6.5–6.8	7.3–7.4
Greatest width (cm)	1.7	1.5–1.6
Wings		
Shape	oblong; apex rounded	oblong; apex acute or rounded
Length (cm)	1.0	1.0–1.1
Width (cm)	0.4	0.4
Keel		
Shape	apex short-apiculate	apex apiculate or emarginate
Length (cm)	0.8	1.0–1.1
Width (cm)	1.0	0.8–1.0

This suggestion requires confirmation by analysis of segregation in the F_2 generation.

The variation in the four F_1 hybrid siblings derived from a single cross, *Erythrina crista-galli* × *E. guatemalensis*, is illustrated in Figures 76–87. The female parent has an irregular network of low lamellae less than 10 μm tall and lacks epicuticular wax. The male parent has a dense covering of unicellular papillae up to 40 μm tall and has epicuticular wax. The F_1 hybrids exhibit a narrowly segregating array of these characters: they have papillae and/or lamellae intermediate in form and stature between the two parents. Some F_1s resemble the female parent more closely and some resemble the male parent. All the F_1s have epicuticular wax, evidently derived from the male parent. (Other individuals of *E. crista-galli*, besides the one used in this cross, do possess wax.)

The leaf epidermis of three F_1 siblings derived from the cross *Erythrina crista-galli* × *E. fusca*, together with their parents, are illustrated in the two plates comprising Figures 88–99. Also included on these plates are photos of *E. dominguezii*, a species that, based on floral characters, may be a stabilized derivative of hybridization between *E. crista-galli* and *E. fusca* (see discussion of hybrid flowers below). The male parent *Erythrina fusca* has a very unusual epidermal surface with deep and irregularly sized and shaped cavities, knobs and protrusions, appearing under SEM much like the surface of a limestone cavern. The stomata are at the bottom of the cavities.

The F_1 hybrids vary somewhat in surface configuration, but none of them possess either the regular network of lamellae present in *E. crista-galli* or the complex, irregular cavity structure of *E. fusca*. Two of the F_1s have scattered low papillae and one is nearly flat on the abaxial surface. All three F_1s have epicuticular platelets, which are not present in either of the parents.

Erythrina dominguezii (Figs. 93, 99) has scattered balloonlike hairs, not present in *E. crista-galli* or *E. fusca*. Otherwise, the epidermal surface on *E. dominguezii* has no distinctive features. Low

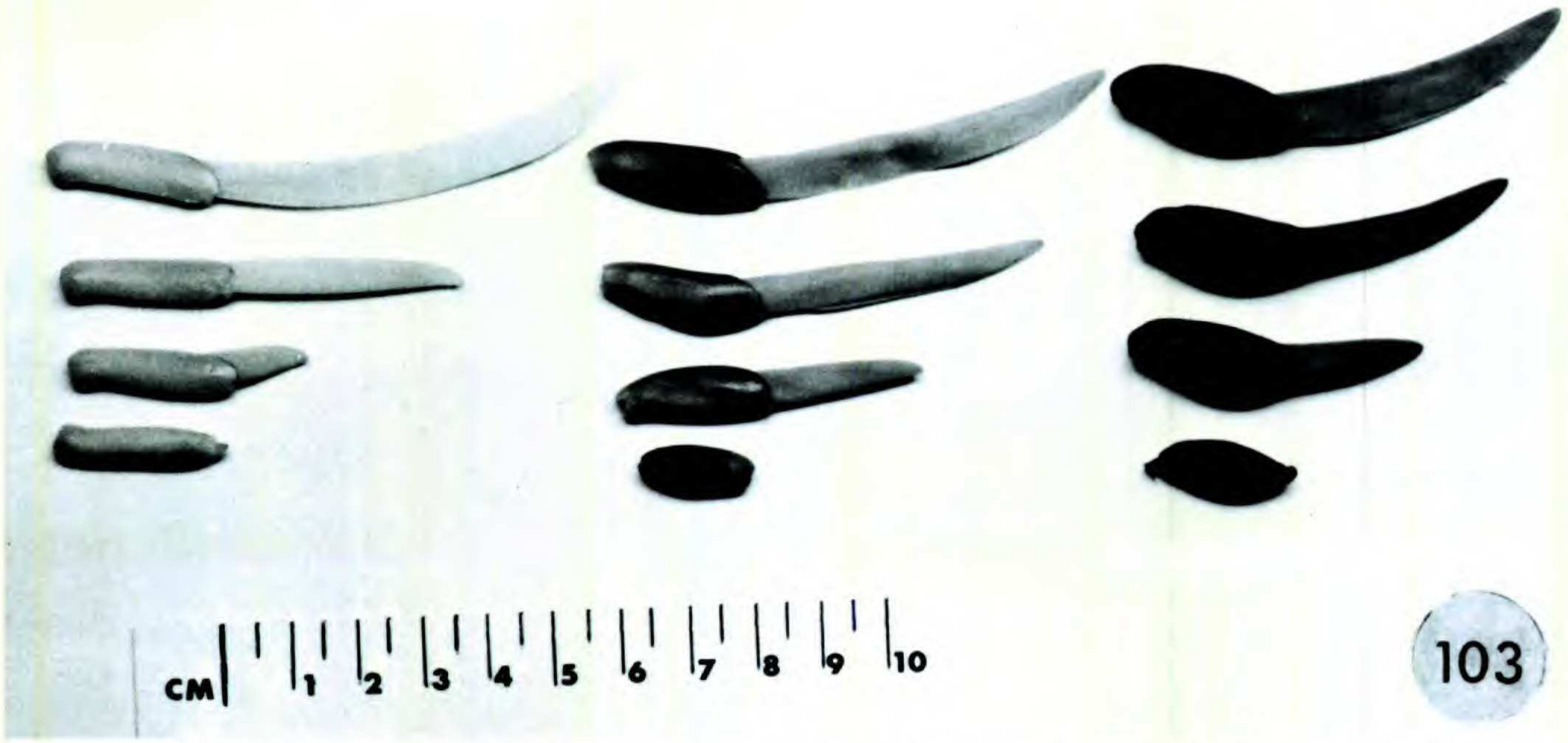


FIGURE 103. *Flowers and buds of* Erythrina berteroana × E. guatemalensis *and parents. Left:* E. berteroana, *WA 78s564, female parent. Center:* E. berteroana × E. guatemalensis, *HO 82.647. Right:* E. guatemalensis, *WA 74c1453, male parent.*

epidermal convolutions similar to the lamellae of *E. crista-galli* are visible at high magnification (Fig. 99) but these are not organized into a regular reticulate pattern.

FLORAL FEATURES: INHERITANCE IN INTERSPECIFIC HYBRIDS

The inheritance of floral morphology and color was examined in the hybrids that flowered by November 1984. These included the hybrids within sect. *Erythrina* and the intersectional hybrid *Erythrina crista-galli* × *E. fusca.*

Materials and Methods

Fresh flowers of the hybrids and parents were fixed in FAA, which preserved their three-dimensional shape, and later measured, described, and photographed, each hybrid together with its par-

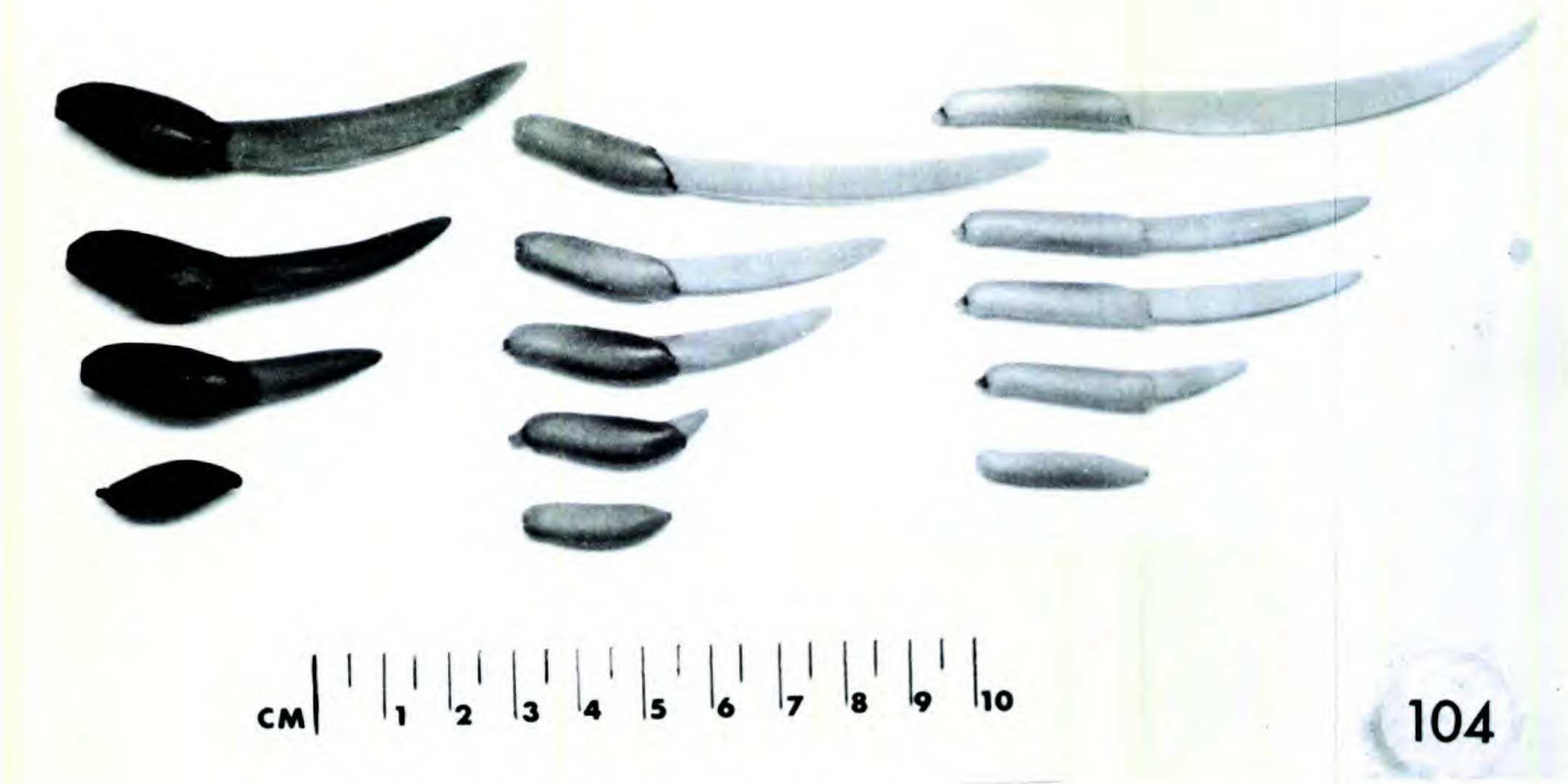


FIGURE 104. *Flowers and buds of* Erythrina guatemalensis × E. tajumulcensis *and parents. Left:* E. guatemalensis, *WA 74c1453, female parent. Center:* E. guatemalensis × E. tajumulcensis, *PT 820547. Right:* E. tajumulcensis, *WA 74c1448, male parent.*

FIGURE 105. *Flowers and buds of* Erythrina guatemalensis × E. folkersii *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. folkersii, *two F_1 siblings, HO 82.282. Right:* E. folkersii, *PT 700010001, male parent.*

ents. Color was determined from fresh flowers at the time of collection. A Berlin & Kay color chart (Berlin & Kay, 1969) was used for color descriptions of corolla standards. For use of the Berlin & Kay color chart in botanical descriptions see Croat (1983). Colors are reported in the form "Red 5/7.5." The number preceding the slash refers to brightness (1–9; 1 is brightest) and the number after the slash refers to the hue.

Inflorescences and floral details were photo-

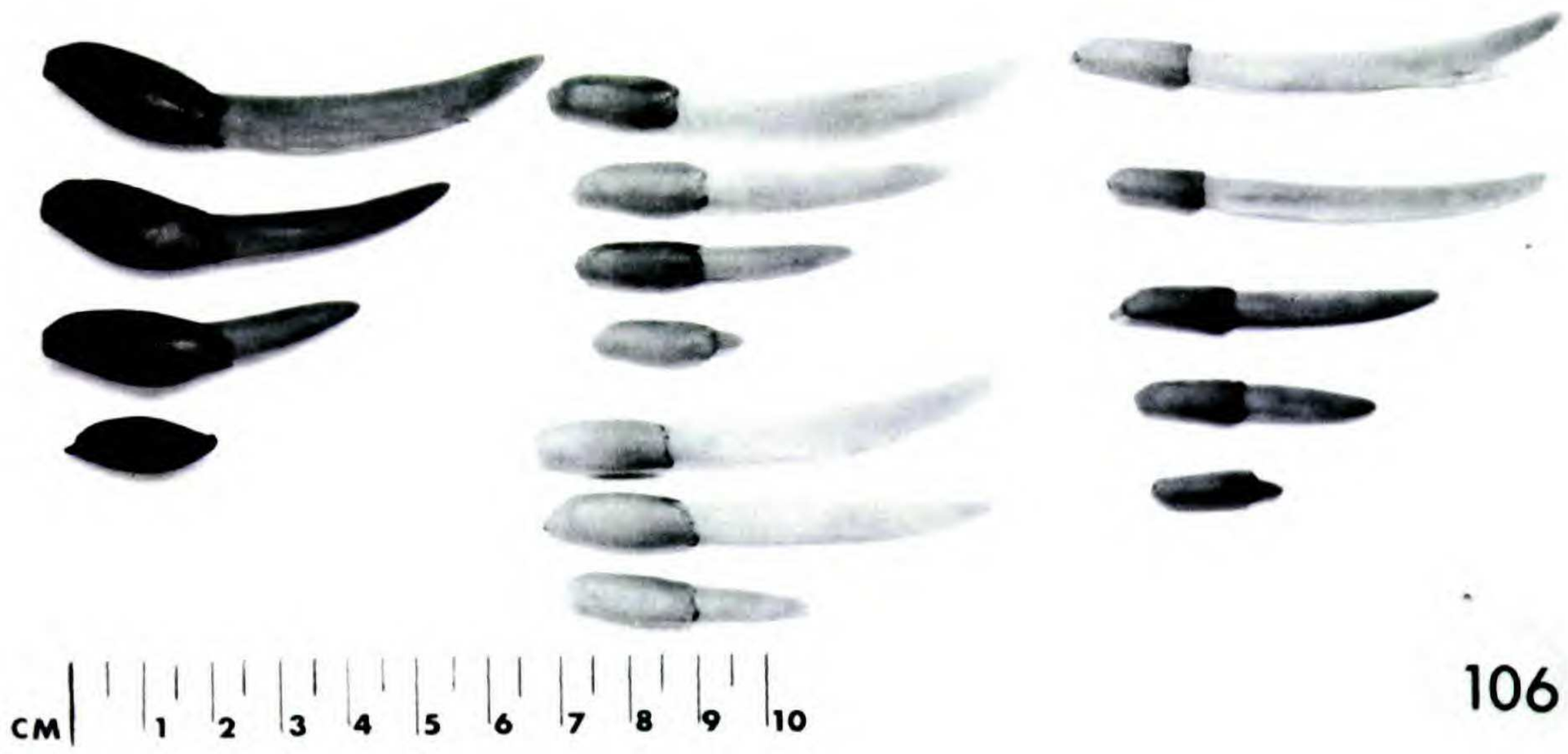


FIGURE 106. *Flowers and buds of* Erythrina guatemalensis × E. chiapasana *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. chiapasana, *two F_1 siblings, HO 82.284 and PT 820278002. Right:* E. chiapasana, *PT 730710001, male parent.*

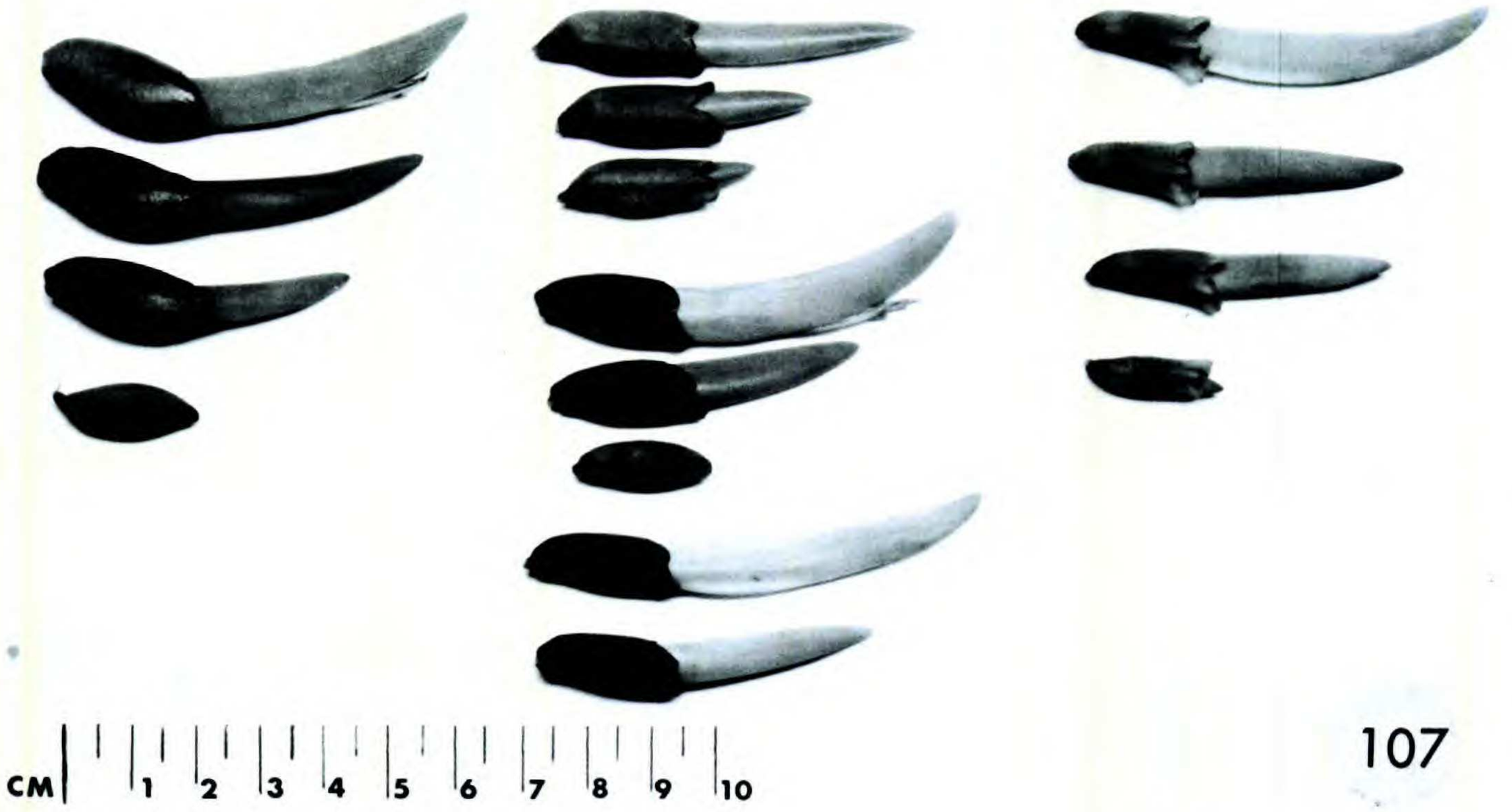


FIGURE 107. *Flowers and buds of* Erythrina guatemalensis × E. macrophylla *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. macrophylla, *three F_1 siblings, HO 82.285, HO 82.288, PT 820276001. Right:* E. macrophylla, *PT 750420002, male parent.*

FIGURE 108. *Flowers and buds of* Erythrina macrophylla × E. guatemalensis *and parents. Left:* E. macrophylla, *PT 750420002, female parent. Center:* E. macrophylla × E. guatemalensis, *two F_1 siblings, HO 82.763. Right:* E. guatemalensis, *PT 700018001, male parent.*

FIGURE 109. *Flowers and buds of* Erythrina chiapasana × E. berteroana *and parents. Left:* E. chiapasana, *PT 721005001, female parent. Center:* E. chiapasana × E. berteroana, *two F_1 siblings, HO 82.278. Right:* E. berteroana, *PT 700044002, male parent.*

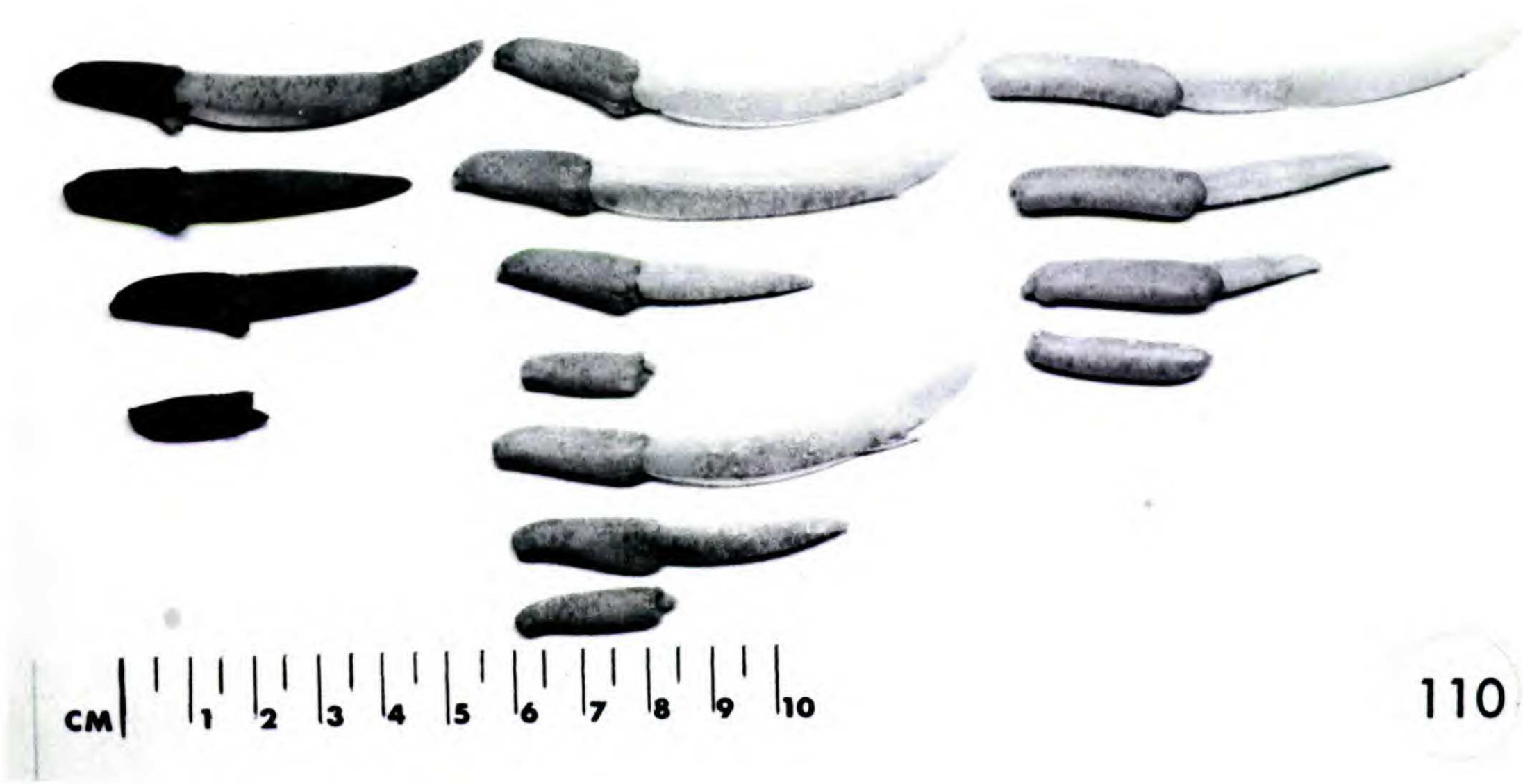


FIGURE 110. *Flowers and buds of* Erythrina macrophylla × E. berteroana *and parents. Left:* E. macrophylla, *PT 750420002, female parent. Center:* E. macrophylla × E. berteroana, *two F_1 siblings, HO 82.281. Right:* E. berteroana, *PT 700044001, male parent.*

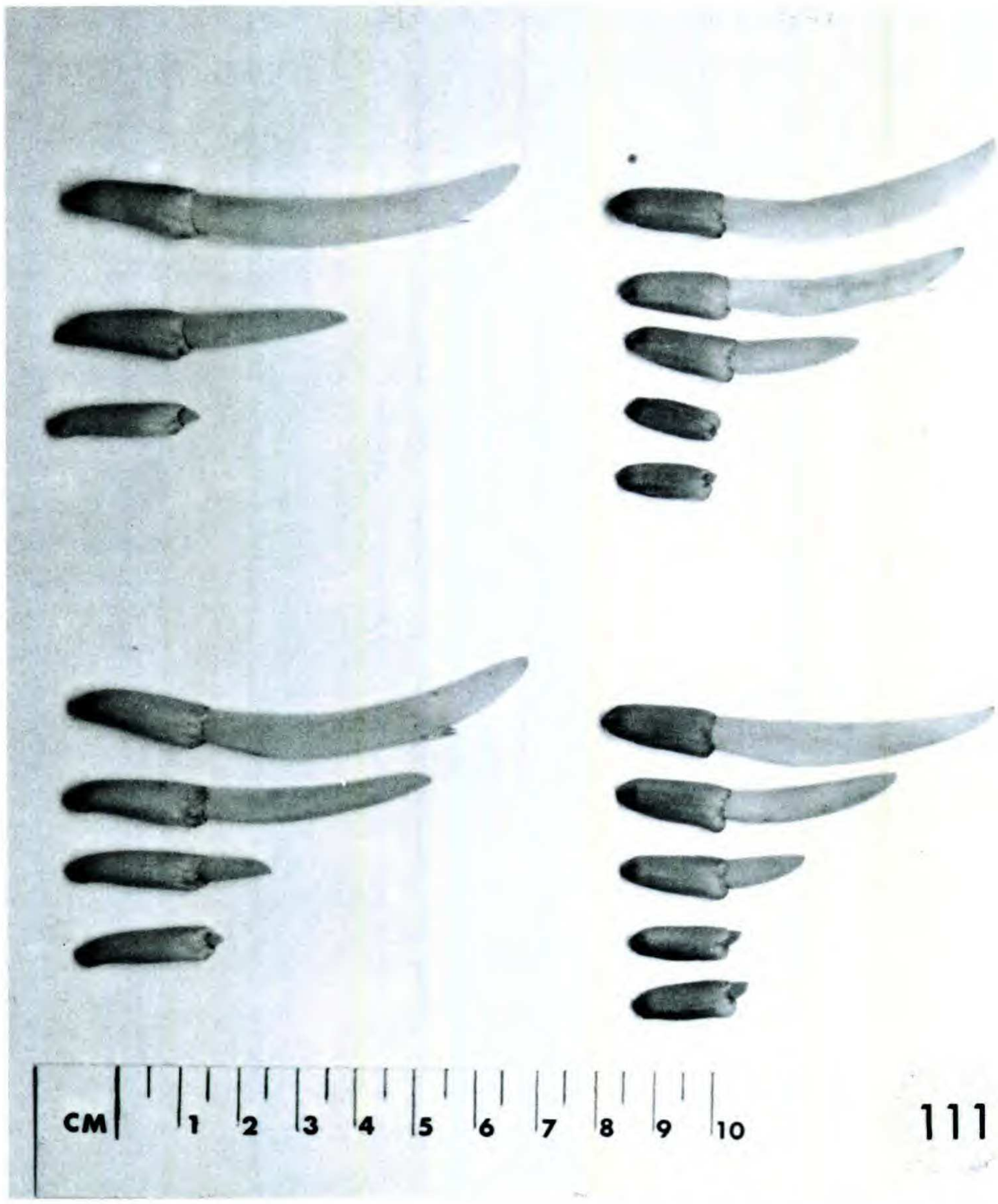


FIGURE 111. *Comparison of flowers of* Erythrina macrophylla × E. berteroana *and* Erythrina atitlanensis. *Left:* E. macrophylla × E. berteroana, *HO 82.281, two F_1 siblings. Top right:* E. atitlanensis, *WA 74s98. Bottom right:* E. atitlanensis, *WA 75s1141.*

graphed at the time of collection. Herbarium vouchers are deposited at Missouri Botanical Garden (MO).

Results

Hybrids within Sect. Erythrina

Inflorescence and Flower Orientation. Species of sect. *Erythrina* all have erect inflorescences, but they differ in the arrangement of the flowers on the inflorescence axis (congested or open), length of the axis, and orientation of the flowers (ascending, horizontal, or descending). These traits are generally intermediate in the hybrids (e.g., Figs. 100–102). In *Erythrina guatemalensis*, the female parent, the flowers are horizontal on an open inflorescence. In *E. folkersii*, the male parent, the flowers descend to nearly vertical on a congested inflorescence. The F_1 hybrid is intermediate in both these traits.

Floral Characters. A comparison of floral characters of the hybrids and their parents within sect. *Erythrina* is summarized in Table 19. The flowers are illustrated in Figures 103–110.

In all characters—color, indumentum, shape, and morphometric dimensions—the F_1 hybrids are intermediate between the two parents. The F_1 siblings from a single cross vary to some extent. There is no evidence of matrocliny or maternal dominance.

Subjectively, some of the hybrids resemble the male parent more closely than the female parent. This is evident in the progeny of the reciprocal hybridizations between *Erythrina guatemalensis* and *E. macrophylla* (Figs. 107, 108). The vestiture and shapes of the calyces of the hybrids are

TABLE 21. *Comparison of flowers of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii.

	E. crista-galli WA 74p840	*E. crista-galli* × *E. fusca* PT 84021001	*E. fusca* PT 840231001	*E. dominguezii* WA 74s865
Orientation	resupinate; standard beneath, open	standard semi-cleistogamous, folded over reproductive parts	standard reflexed	standard semi-cleistogamous, folded over reproductive parts
CALYX				
Color	red	reddish brown	brown	pale orange-pink
Shape	bowl shaped	bowl shaped; slightly asymmetric	asymmetrically bowl shaped	asymmetrically bowl shaped
Length				
Carinal side	1.8 cm	1.6 cm	1.4 cm	1.5 cm
Width at apex	1.0 cm	1.4 cm	2.1 cm	1.4 cm
Apex ornamentation	large subulate tooth, carinal side	narrow tooth, carinal side	large blunt tooth, carinal side	blunt tooth, carinal side
COROLLA				
Standard				
Color	red	orange	orange-pink	pale orange-pink
Length	5.0 cm	6.1 cm	6.5 cm	4.8 cm
Width	3.3 cm	4.9 cm	5.5 cm	3.5 cm
Wings				
Shape	asymmetric; broadest at base	obovate, rounded, cucullate	obovate, cucullate, broadly rounded	small, obovate, cucullate
Length	1.3 cm	1.8 cm	2.9 cm	0.6 cm
Width	0.9 cm	1.0 cm	1.8 cm	0.4 cm
Keel				
Color	red	pale red	ivory at base, red at apex	pale red
Shape	falcate, acute at apex	ovate-falcate, rounded at apex	ovate-falcate, broadly rounded at apex	falcate, acute at apex
Length	4.5 cm	3.4 cm	3.9 cm	1.5 cm
Width	1.0 cm	1.5 cm	1.5 cm	1.0 cm

intermediate and variable, but in both reciprocals the hybrids resemble the male parent somewhat more than the female.

In crosses involving species with tomentose and glabrous calyces, the hybrids are tomentose, but sometimes sparsely so. In color values and morphometric dimensions, the hybrids are generally intermediate between the two parents.

The flower of the hybrid *Erythrina macrophylla* × *E. berteroana* is intermediate between the two parents, and it closely resembles a third recognized species, *E. atitlanensis* (Fig. 111, Table 20). The principal difference is that the calyx of the F_1 hybrid is somewhat longer than that of *E. atitlanensis*. The natural distribution of *Erythrina atitlanensis* is confined to a small area near Lake Atitlan in western Guatemala, and it is geographically and ecologically intermediate between *E. macrophylla* and *E. berteroana*. The possibility that the form known as *E. atitlanensis* represents either a hybridizing population or a stabilized species of hybrid origin will be discussed below.

Flowers of Erythrina crista-galli × E. fusca

The inflorescence and flowers of this intersectional hybrid and its parents are illustrated in Figures 112–117 and described in Table 21. A third species, *E. dominguezii*, is included in the illustrations and descriptions for reasons discussed below.

The morphometric dimensions and proportions of the floral parts of the two parental species are relatively similar, considering the total range of

FIGURES 112–115. *Inflorescences in natural position of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii.—*112.* E. crista-galli, *WA 74p840.*—*113.* E. fusca, *WA 74s99.*—*114.* E. crista-galli × E. fusca, *PT 840231001.*—*115.* E. dominguezii, *PT 740234001.*

variation of these traits in the genus *Erythrina*, but the way in which these parts are arranged and the overall appearance of the flowers are very different. The flower of *E. crista-galli* is resupinate (inverted from the usual position, with the standard below the keel) and the red standard is flattened out, an unusual trait in *Erythrina*. The orange standard of *E. fusca* is reflexed from the clawed base, exposing the reproductive parts, and is broadly folded down the middle.

The flower of the F_1 hybrid *E. crista-galli* × *E. fusca* is different from either parent. The hybrid flower is semicleistogamous, with the standard tightly folded over the wings, keel, and reproductive parts. In this semicleistogamous form, in the orientation of the flowers and the inflorescence, and in the pale pink-orange color of the corolla standard, *E. crista-galli* × *E. fusca* bears a striking resemblance to *E. dominguezii* (Figs. 114–117). Certainly the hybrid resembles *E. dominguezii* more closely in overall appearance than either of its parents. The dimensions of the floral parts are not identical in the F_1 hybrid and in *E. dominguezii* (Fig. 117, Table 21). The overall similarity between the two could be a coincidence, but it is so striking and so unexpected that it raises the possibility that *Erythrina dominguezii* is in fact a hybrid derivative of *E. crista-galli* and *E. fusca*. The distribution of *E. dominguezii* is geographically intermediate but ecologically distinct from *E.*

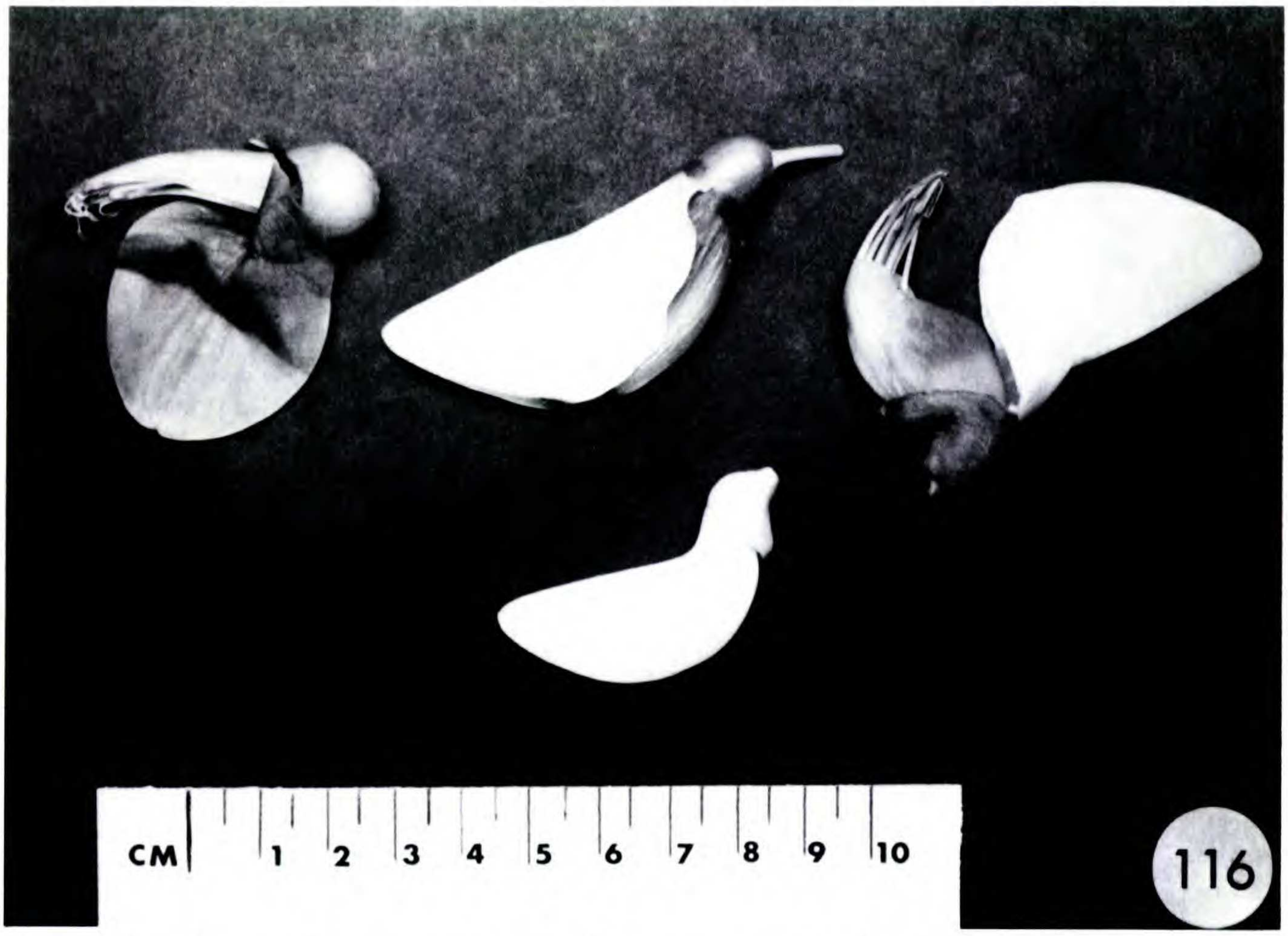


FIGURE 116. *Flowers of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii, *showing approximate natural orientation. Top row, left to right:* E. crista-galli, *WA 75p840, female parent;* E. crista-galli × E. fusca, *PT 840231001;* E. fusca, *WA 74s99, male parent. Bottom center:* E. dominguezii, *PT 740234001.*

crista-galli and *E. fusca*. This will be discussed in greater detail in Section 6.

Conclusions: Inheritance of Phenetic Traits in Interspecific Hybrids

The results of the morphological studies of the F_1 hybrids clearly demonstrate that the progeny are indeed of hybrid origin. Almost universally, the F_1 progeny meet the criterion of intermediacy, and frequently they possess traits present in the male parent but absent in the female parent. Matrocliny is not indicated in *Erythrina* hybrids. Some of the F_1 hybrids closely resemble forms occurring in natural populations and recognized as species.

SECTION 6. NATURAL HYBRIDIZATION AND HYBRID SPECIATION

The Mexican state of Chiapas has great geographical diversity and complexity and a very large flora for an area its size. Climate ranges from semidesert to rainforest, and elevation from sea level to over 4,000 m. The flora of Chiapas contains more than 8,000 plant species and 13 major vegetational formations recognized by Breedlove (1981).

Chiapas, together with adjacent western Guatemala, is also the center of diversity of *Erythrina* sect. *Erythrina*. Eleven species are known to occur in the state, and six of these are endemic or shared only with western Guatemala. Although they are not found in abundance or in large populations, species of *Erythrina* occur in virtually every vegetation type in Chiapas except the upper belts of the cloud forest and elfin forest on the highest peaks.

In common with the usual pattern of distribution in *Erythrina*, the Chiapas species of the genus are mostly allopatric. However, at some localities, particularly at the margins of distribution of the species, different species do come into contact, and there natural hybrids are formed.

One phenomenon that has apparently occurred with *Erythrina* in Chiapas and perhaps elsewhere is spontaneous hybridization in man-made populations. Throughout Mesoamerica many species of *Erythrina* trees are used by the local populace as "living fenceposts." Erythrinas take root readily from woody cuttings and the trunks are ideal posts for stringing barbed wire. Extensive fencerows of the plants line roads and fields in many areas.

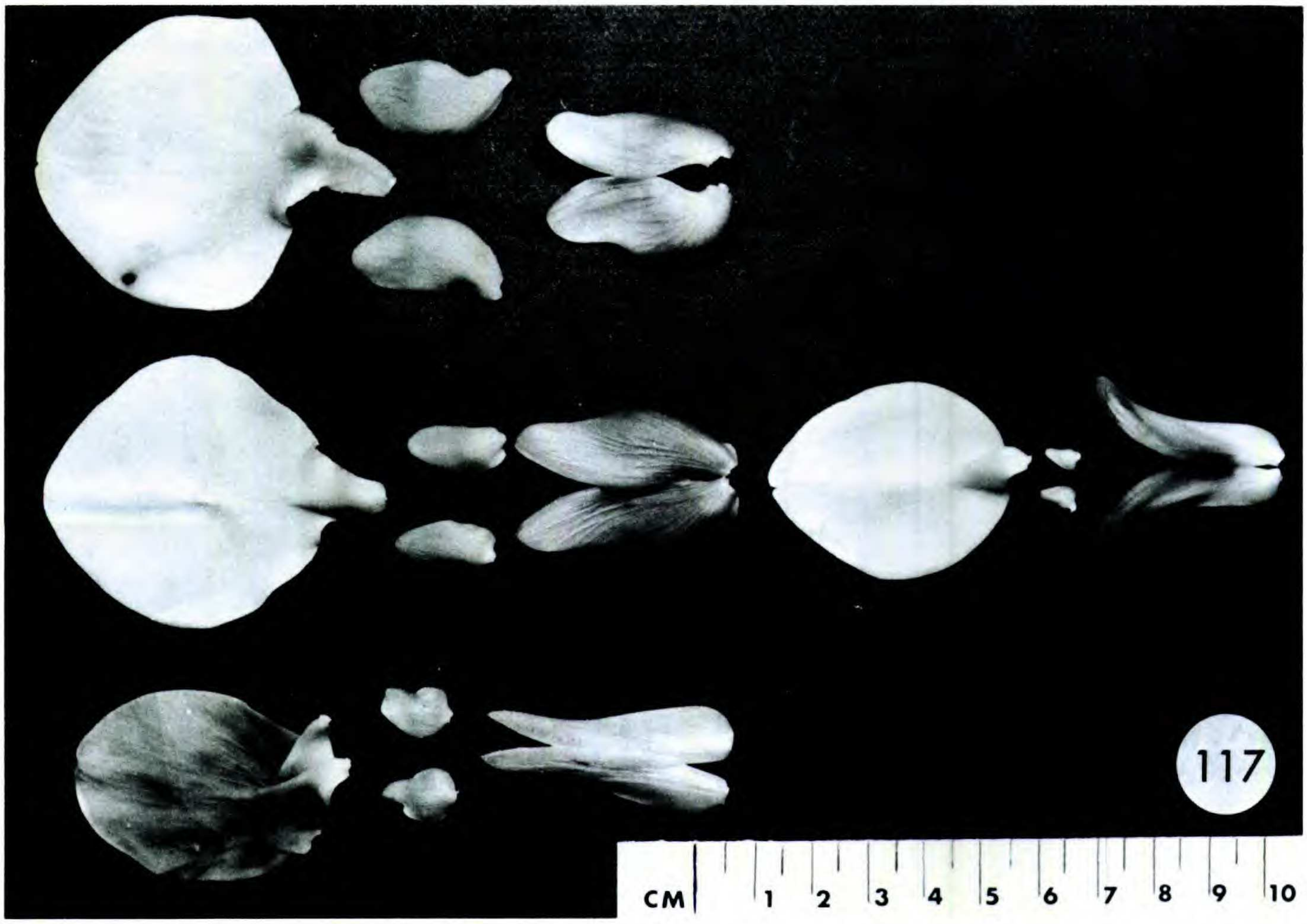


FIGURE 117. *Dissected petals of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii *(each flower, left to right: standard, wings, keel). Top:* E. crista-galli, *WA 74p840, female parent. Center left:* E. crista-galli × E. fusca, *PT 840231001. Center right:* E. dominguezii, *PT 740234001. Bottom:* E. fusca, *WA 74s99, male parent.*

Sometimes two species are cultivated together, and hybrids, apparently produced spontaneously in situ, are occasionally found in these fencerows.

An analysis of hybridizing populations involving three species of *Erythrina* in central Chiapas, *Erythrina chiapasana*, *E. goldmanii*, and *E. pudica*, is presented below. Distributions of these species and their hybrid populations are shown in Figure 118.

Erythrina chiapasana × *E. goldmanii*

Erythrina chiapasana is a tree of the pine–oak forests of the Central Plateau of Chiapas, occurring primarily above 1,500 m. *Erythrina goldmanii* inhabits the dry tropical deciduous forests of the Central Depression of Chiapas, formed by the highland-rimmed valley of the Río Grijalva. At El Sumidero National Park a few km north of the city of Tuxtla Gutierrez, where the Río Grijalva cuts through the limestone of the Central Plateau on its way to the Atlantic Ocean and forms a spectacular 800-m-deep canyon, the two species occur parapatrically and a hybrid zone is found about 2 km wide and extending about 300 m along an elevational gradient (Fig. 119).

Throughout their respective distributions, *Erythrina chiapasana* and *E. goldmanii* exhibit some intraspecific variation, but the two species are readily distinguishable morphologically. The leaves of *E. chiapasana* are densely tomentose with two-armed hairs on the abaxial surface (Fig. 120). The leaves of *E. goldmanii* are glabrous or nearly so at maturity and are aculeate along the midvein and primary veins of the abaxial surface (Fig. 122). The calyx of *E. chiapasana* is green to reddish, densely puberulent, and truncate at the margin without a prominent tooth on the carinal side; the corolla standard is dark red. The calyx of *E. goldmanii* is broader, dark purple brown to nearly black, glabrous, and provided with a prominent apical tooth on the carinal side; the corolla standard is usually pale red.

At El Sumidero both species are at the altitudinal and geographical limits of their ranges. Only individuals with the "pure" *E. chiapasana* phenotype are found in the oak-dominated forest at the plateau summit above 1,100 m; only individuals

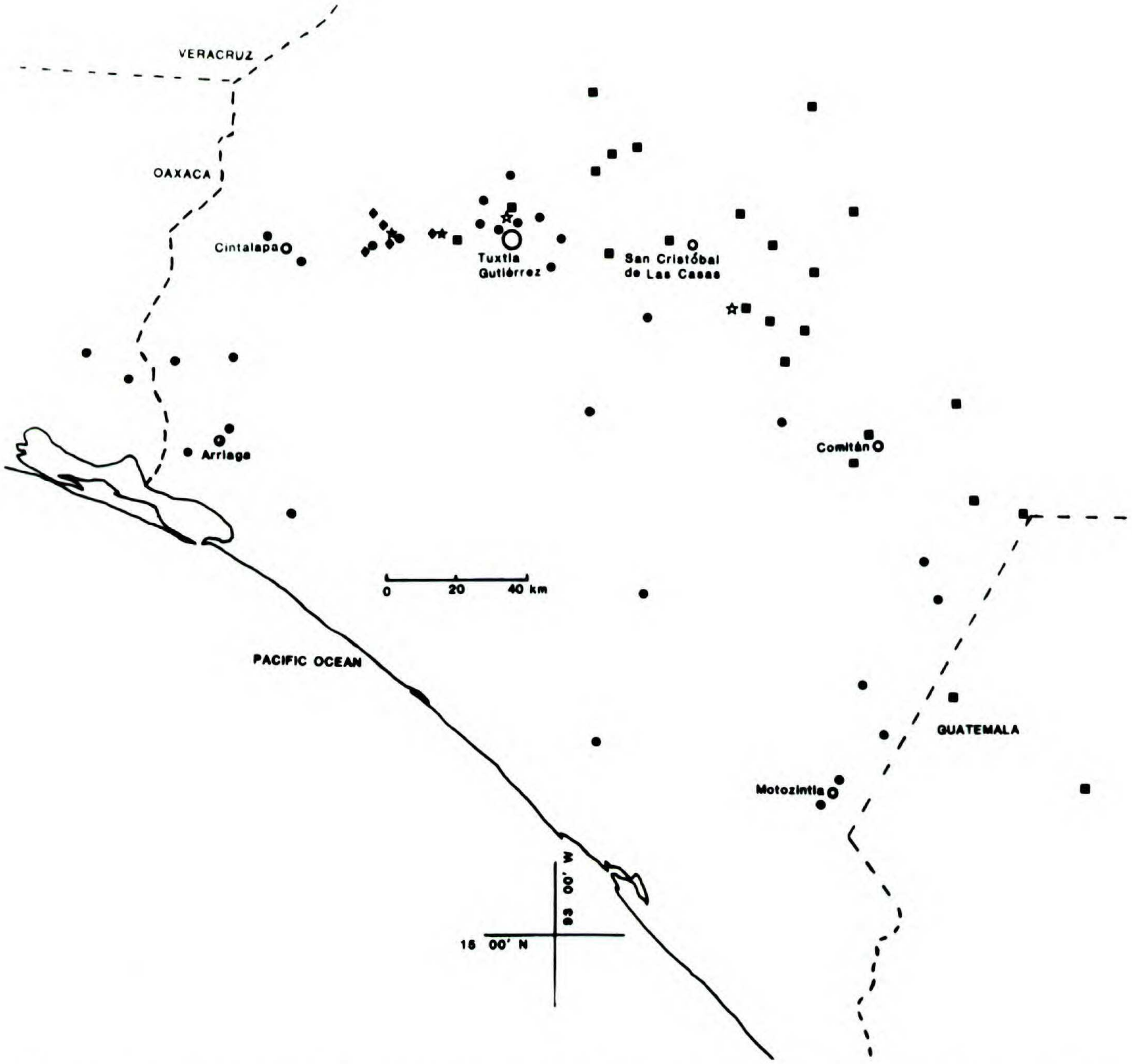


FIGURE 118. *Distribution of* Erythrina chiapasana, E. goldmanii, E. pudica, *and hybrid populations in Chiapas, Mexico. Squares*—E. chiapasana; *circles*—E. goldmanii; *diamonds*—E. pudica; *open stars*—E. chiapasana × E. goldmanii; *solid stars*—E. goldmanii × E. pudica.

with the "pure" *E. goldmanii* phenotype are found in the dry scrub forest below 800 m. In the transition zone near the top of the escarpment between 800 m and 1,100 m there are plants with intermediate phenotypes, or displaying in one individual various combinations of traits of both species. Some individuals, for example, have leaves that are sparsely tomentose on the abaxial surface and are also aculeate on the midvein (Fig. 121). Others have flowers with characters intermediate between the two species, or with various combinations of parental traits such as a puberulent, dark purple-brown calyx with an apical tooth (Fig. 123). Both parental types are also present in the transition zone.

This pattern of variation in the intermediate zone at El Sumidero establishes with reasonable certainty that the population is a hybrid swarm of *Erythrina chiapasana* × *E. goldmanii*. The intermediacy of the traits in this population resembles the patterns of inheritance expressed in the experimentally produced hybrids as discussed in Section 5.

As indicated in Section 4, I attempted to synthesize hybrids between *Erythrina chiapasana* and *E. goldmanii* in the field at El Sumidero using the same techniques of controlled hand-pollination employed in the experimental gardens in Hawaii. Hybrid fruits in both reciprocal crosses were obtained, but the fruit of *Erythrina chiapasana* ♀ × *E. goldmanii* ♂ was destroyed in a brush fire. The reciprocal *E. goldmanii* ♀ × *E. chiapasana* ♂ produced one mature hybrid seed. The F_1 was viable and is now growing in cultivation in Hawaii

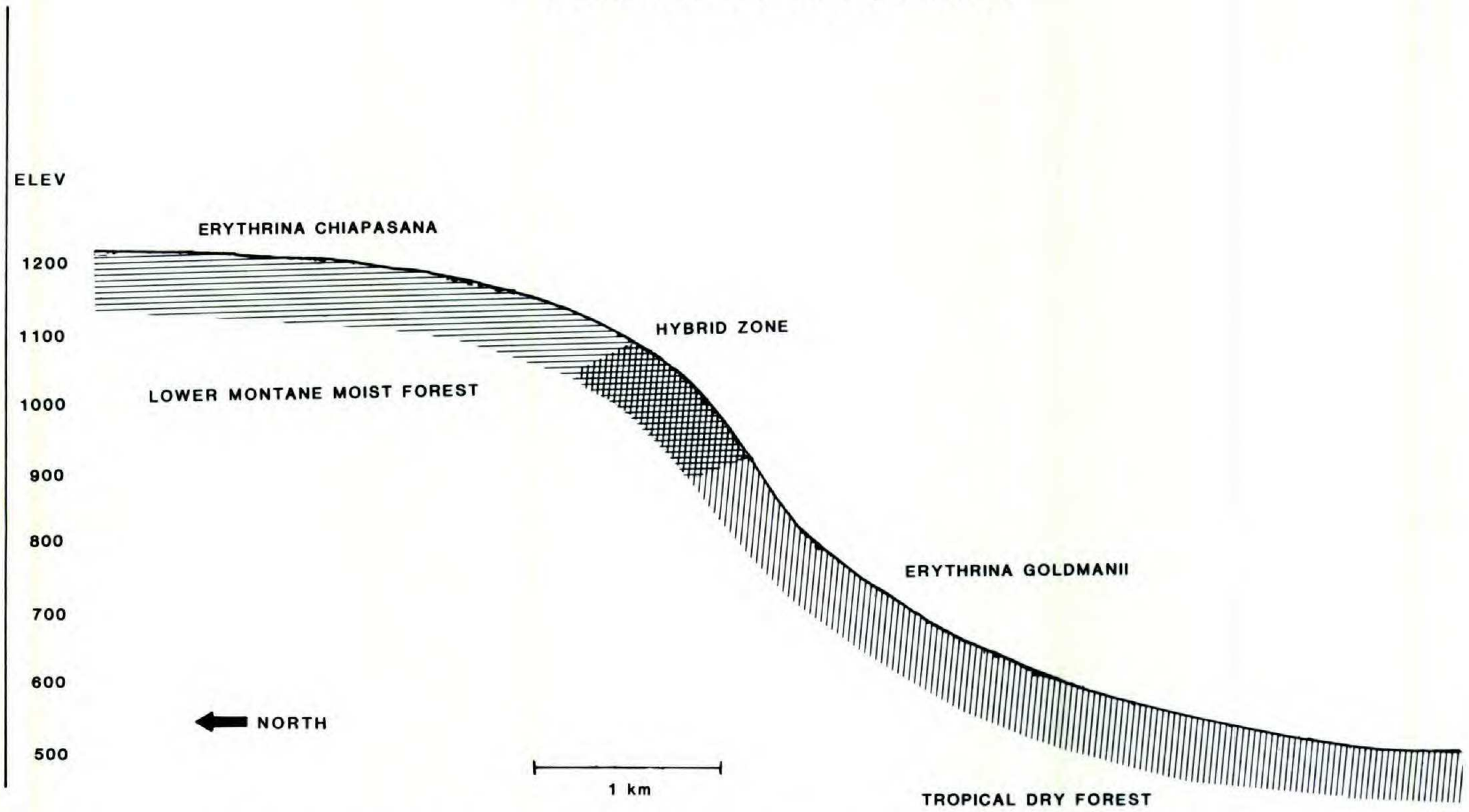


FIGURE 119. *Cross section of slope at El Sumidero, Chiapas, Mexico, showing distribution of* Erythrina chiapasana, E. goldmanii, *and hybrid zone.*

alongside accessions of both parental strains (Table 11). When this artificial hybrid flowers it will be possible to compare it with specimens of the putative natural hybrids from El Sumidero.

As discussed in a separate paper (Neill, 1987), the hummingbird *Heliomaster constantii* pollinates *Erythrina chiapasana* and *E. goldmanii* at El Sumidero and is therefore implicated as the agent directly responsible for interspecific gene flow in the hybridizing *Erythrina* population.

Erythrina goldmanii × *E. pudica*

Erythrina pudica is a locally endemic species that is restricted to the dry valley of the Río de La Venta, a tributary of the Río Grijalva, at the western end of the Central Depression of Chiapas. This is an unusual species, with the flowers drooping to nearly parallel with the erect axis of the inflorescence (Fig. 126). The calyx is truncate without an apical tooth and covered with a dense grayish tomentum; the corolla is very pale pink or orange-pink.

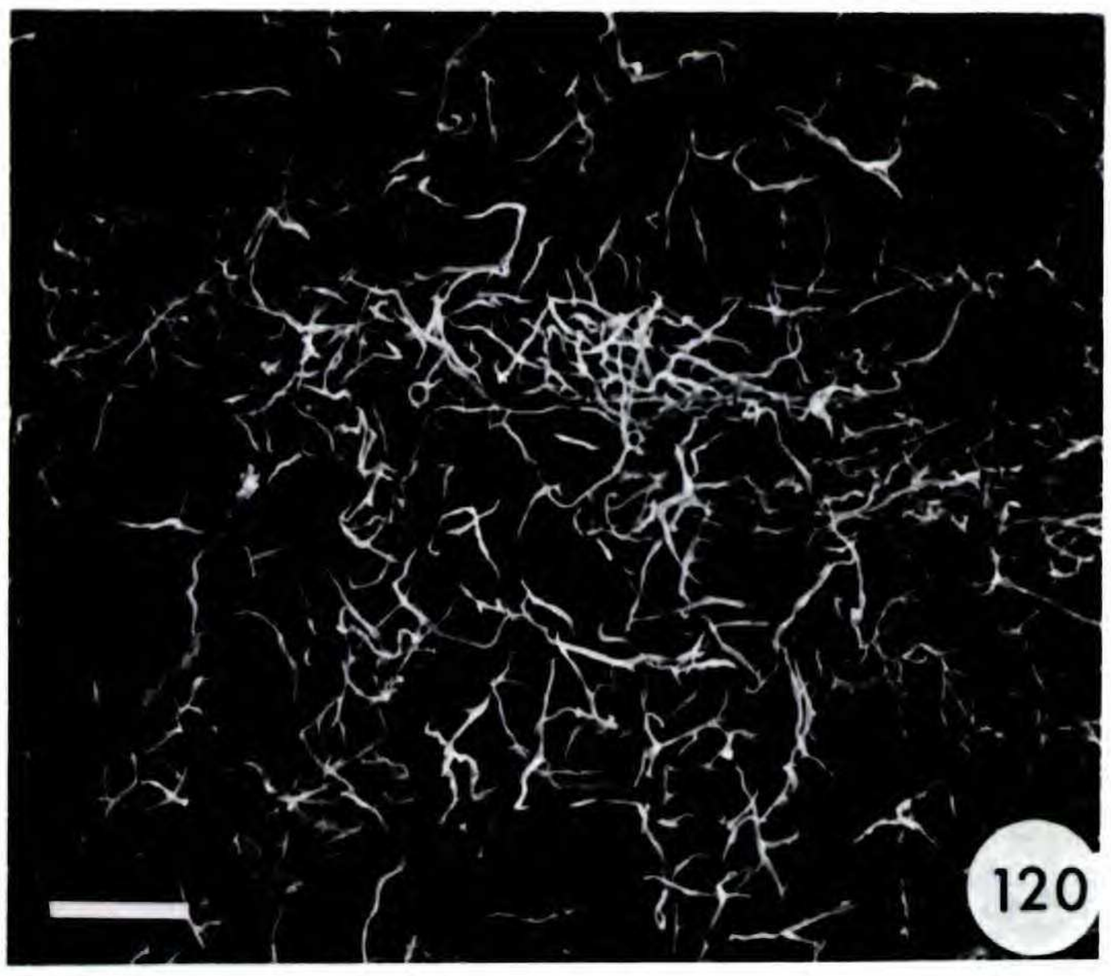
In the vicinity of Ocozocuautla, Chiapas, at the eastern margin of its small range, *Erythrina pudica* occurs sympatrically with *Erythrina goldmanii*. In disturbed scrub forest small hybrid populations are found, with individuals of both parental species as well as intermediates (Figs. 124–126).

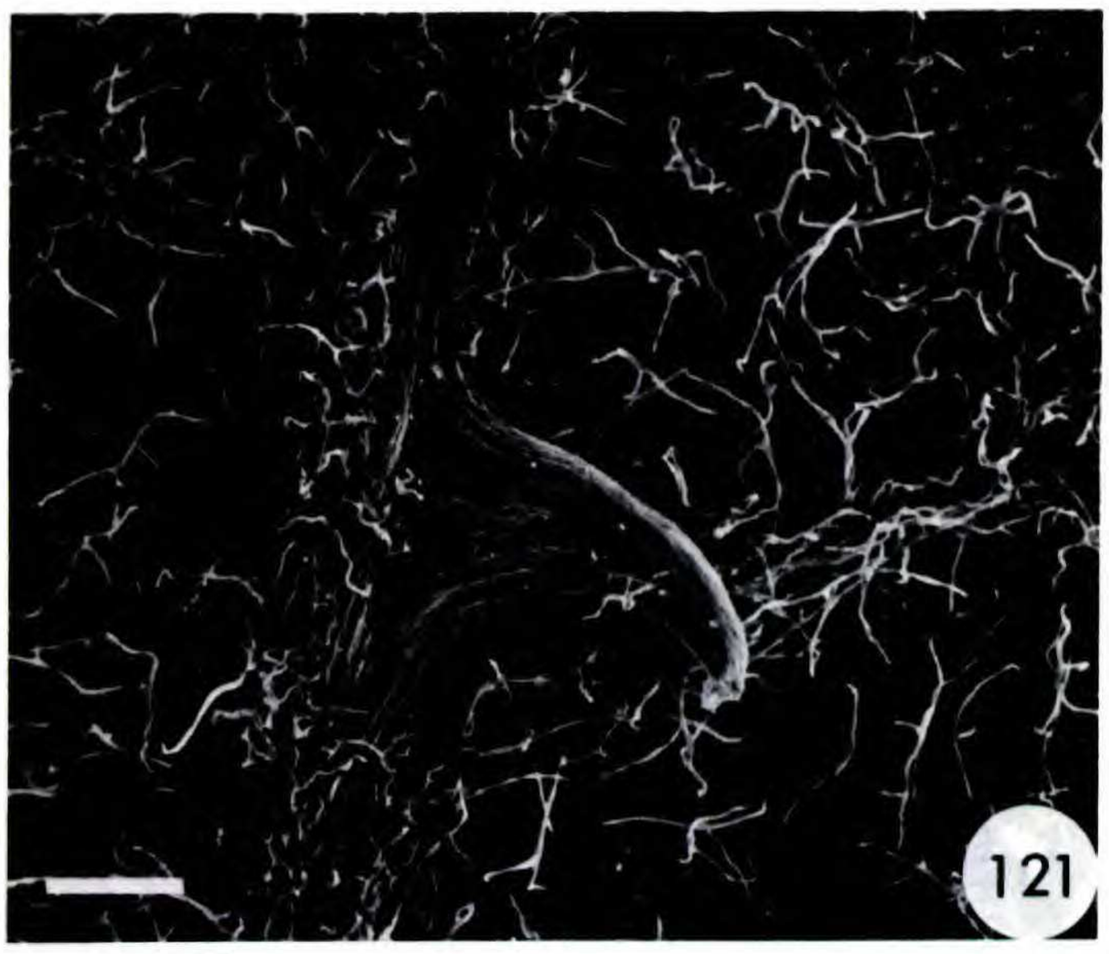
Along the highway 5 km east of Ocozocuautla are living fencerows of *Erythrina* containing both *E. goldmanii* and *E. pudica*, and occasional intermediate and evidently hybrid individuals occur there. These intermediates are similar in appearance to the trees occurring in the adjacent natural hybrid populations. The fencepost hybrids are very likely the progeny of other fencepost trees that received interspecific pollen from foraging hummingbirds moving down the line of mixed species fenceposts. The hybrid seed thus probably germinated directly below its female parent and grew up to become part of the fencerow itself.

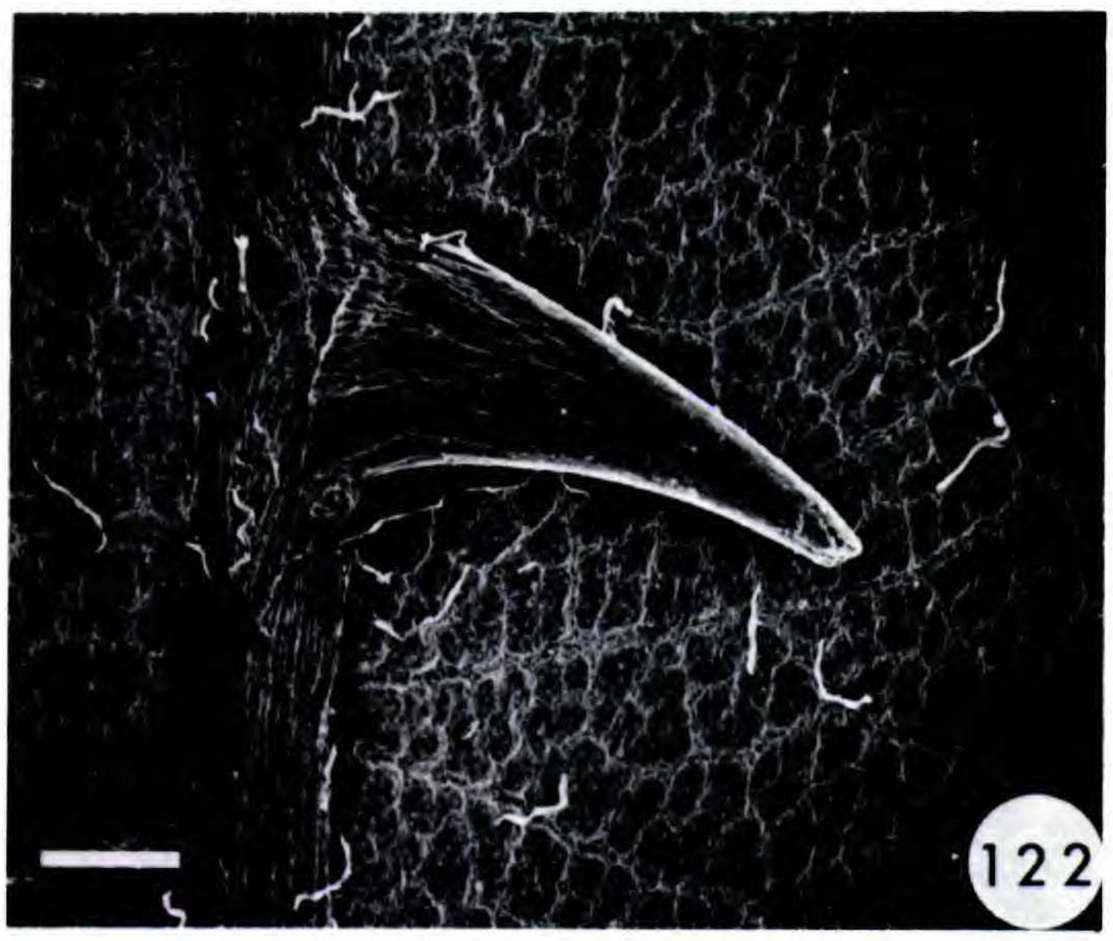
Erythrina berteroana × *E. folkersii*

On the Atlantic coastal plain of northern Chiapas and adjacent states the natural vegetation has been almost entirely destroyed and replaced with pastures. There, as elsewhere in Mesoamerica, the pastures and roadsides are commonly lined with living fencerows of *Erythrina* trees. On the Atlantic plain the most frequently used species are *E. berteroana* and *E. folkersii*, which are both native to the region.

Trees morphologically intermediate between *Erythrina berteroana* and *E. folkersii* in shape and vestiture of the calyx and orientation of the flower occur in northern Chiapas. None of the intermediates set seed. Pollen stainability from four collections of the intermediates (Alexander's stain; 500 grains per sample: *Neill 5533, 5540, 5543, 5544*) was 73.2% (range 60.9–86.1%), an un-







FIGURES 120–122. *SEM images, abaxial leaf surfaces of* Erythrina chiapasana, E. goldmanii, *and hybrid from a population at El Sumidero, Chiapas, Mexico.— 120.* E. chiapasana, Neill 5617.—*121.* E. chiapasana × E. goldmanii, Neill 5618.—*122.* E. goldmanii, Neill 5616. *Scale bars = 0.5 mm.*

usually low figure for *Erythrina*. These individuals are almost certainly hybrid *Erythrina berteroana* × *E. folkersii*. The reason for the low level of stainable pollen and lack of fruit set is not known; the experimentally produced hybrids within sect. *Erythrina* (Section 4) all had very high pollen fertility.

These intermediates closely match the type specimen of *Erythrina caribaea* Krukoff & Barneby as well as other collections determined by Krukoff as this species. Despite a protracted search, I never found this form occurring in a natural population and never found any seed set on the fencepost trees. It seems reasonable that *Erythrina caribaea* is in fact a hybrid *E. berteroana* × *E. folkersii* and probably occurs only as a cultivated fencepost tree.

HYBRID SPECIATION

In this paper it has been demonstrated that diploid *Erythrina* species are interfertile, that the hybrids are viable and fertile, and that hybridization sometimes occurs in natural populations. What has not yet been shown is the validity of the final hypothesis set forth in the introductory chapter: that hybrid speciation has taken place in *Erythrina*, that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species, and that this process has been an important element in the evolutionary history of the genus.

Direct and unequivocal evidence relating to this hypothesis is difficult to obtain. Phylogenies based on molecular data of the taxa involved, including studies on isoenzymes and on nucleic acid restriction sites, might in the future provide such evidence. The best evidence available at present is the morphological congruence between certain artificially produced hybrids and certain naturally occurring forms that evidently are stabilized and self-perpetuating populations.

In considering the hypothesis of hybrid speciation, there is no reason to assume that the stabilized derivatives, especially if they became stabilized several generations or more after the original hybridization event, should be precisely intermediate between the parental species or should resemble closely the F_1 hybrids. A limited number of F_1 hybrids is, however, generally the only material available for comparison.

In *Erythrina* some of the artificial F_1 hybrids do resemble naturally occurring forms recognized as species, according to the results of the morphological studies presented in Section 5. *Ery-*

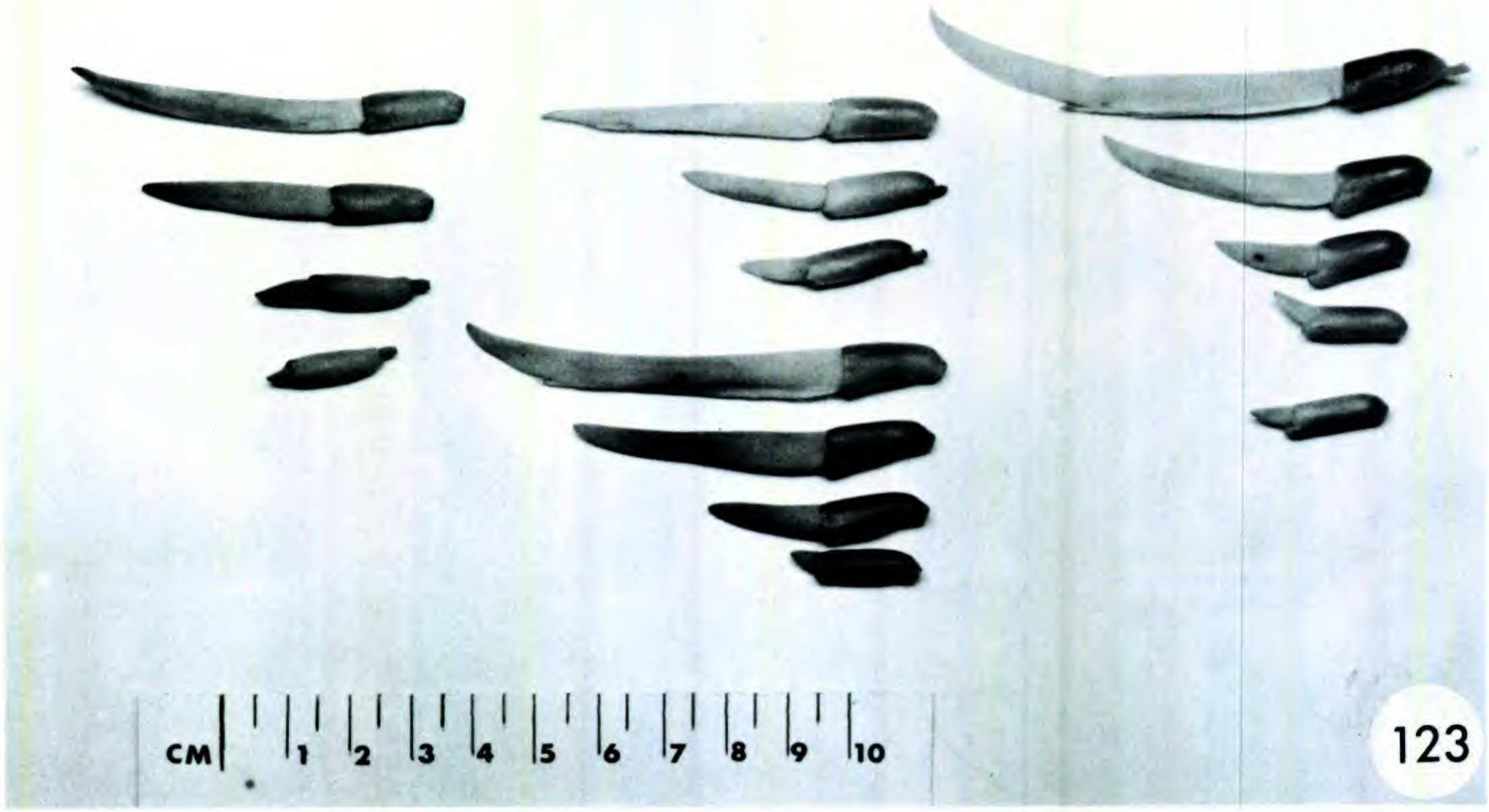


FIGURE 123. *Flowers of* Erythrina chiapasana, E. goldmanii, *and hybrid from a population at El Sumidero, Chiapas, Mexico. Left:* E. chiapasana, Neill 5455. *Center top:* E. chiapasana × E. goldmanii, Neill 5493. *Center bottom:* E. chiapasana × E. goldmanii, Neill 5466. *Right:* E. goldmanii, Neill 5495.

thrina macrophylla × *E. berteroana* bears a close resemblance to *E. atitlanensis*, and *E. crista-galli* × *E. fusca* resembles in certain features *E. dominguezii*. Field studies, which would be valuable for determining whether hybrid speciation could have occurred, were not conducted in either of these situations. The known geographical and ecological distribution of the taxa involved is outlined below.

Erythrina macrophylla is distributed throughout the highlands of Guatemala and western El Salvador, growing in the pine–oak forests above 1,500 m elevation. *Erythrina berteroana*, the most widespread species in sect. *Erythrina*, is common in the Pacific coastal plain of Guatemala and on the lower slopes of the volcanic range that lead up from the plain to the highlands. The intermediate known as *Erythrina atitlanensis* is known only from the vicinity of Lake Atitlan on the southern edge of the highlands. In terms of geography and elevational distribution, *E. atitlanensis* is precisely intermediate between the putative parental species. If hybridization is really implicated in this case, *E. atitlanensis* could be merely an early generation segregate rather than a stabilized, self-perpetuating derivative. Based on comparison of herbarium specimens, the progeny cultivated in Hawaii grown from seed obtained from the population in Guatemala closely resemble the parents. Therefore stabilization of the hybrid form may have taken place.

The case of *Erythrina dominguezii* and its putative parental species *E. crista-galli* and *E. fusca* is more problematic because the three taxa are so morphologically distinct. They are also ecologically distinct. *Erythrina crista-galli* and *E. fusca* are both riparian or estuarine species. *Erythrina crista-galli* is common along the estuary of the Río de La Plata and its tributaries and along the coast of southern Brazil. The more tropical *E. fusca* is distributed widely throughout the Amazon basin and south along the coast of Brazil. The ranges of the two species evidently do overlap in southern Brazil. The putative derivative *Erythrina dominguezii* also occurs in southern Brazil and westward through Paraguay and northern Argentina to eastern Bolivia, but it is an upland species of the dry Chaco forest and cerrado. *Erythrina dominguezii* would never have been suspected as a hybrid derivative of *E. crista-galli* × *E. fusca* were not its resemblance to the artificially produced F_1 so compelling. This situation appears to merit further investigation.

SUMMARY AND CONCLUSION

In the introduction, a set of five hypotheses was stated regarding the species relationships and evolutionary history of *Erythrina*: 1) The numerous species of sect. *Erythrina* can all cross freely with one another, producing fully fertile hybrids. The section forms a homogamic complex in which in-

FIGURES 124–126. *Inflorescences of* Erythrina goldmanii, E. pudica, *and hybrid from a population near Ocozocuautla, Chiapas, Mexico.—124.* E. goldmanii, Neill 5510.—*125.* E. goldmanii × E. pudica, Neill 5586.—*126.* E. pudica, Neill 5585.

ternal barriers to hybridization are absent. 2) The interfertile homogamic complex of sect. *Erythrina* extends, to a greater or lesser degree, to species in other sections and subgenera of *Erythrina*. Any diploid *Erythrina* species can hybridize with any other, but crosses between widely divergent taxa are generally difficult to obtain and the resulting F_1s may exhibit varying degrees of sterility. The genus as a whole may be characterized as a series of interfertile homogamic complexes with weak to moderate reproductive barriers between the complexes. 3) The widely foraging hummingbirds that pollinate species of sect. *Erythrina* are capable of effecting interspecific pollen flow between sympatric species of sect. *Erythrina*. 4) Sympatry at the local community level is rare among species of sect. *Erythrina*. Most species are restricted in geographic range and ecological amplitude and are allopatric, separated by habitat differences. However, sometimes different species do come into contact in nature, and then hybridizing populations are formed. 5) Patterns of distribution and phenetic

variation in sect. *Erythrina* indicate that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species. As a consequence of changing climates and dynamic geomorphological processes, and the consequent migration of vegetation types and mixing of floristic elements, formerly allopatric species may have come into contact a number of times. With the temporary breakdown of external isolating barriers, the interfertile species hybridized and the subsequent segregation and stabilization of hybrid derivatives have contributed to the proliferation of species of *Erythrina*.

The data presented in this paper have been marshalled in support of this set of hypotheses. The cytological studies (Section 3) and the experimental hybridization and self-compatibility trials (Section 4) present evidence in support of the first two hypotheses. In spite of the considerable morphological, ecological, and geographic differentiation of *Erythrina*, the species have retained a high degree of chromosomal (structural and genic) homology. Within sect. *Erythrina*, this homology, as evidenced by interspecific compatibility, is virtually complete: there is no detectable difference in the success of interspecific matings as compared with intraspecific matings. At greater taxonomic distances between the two parents (intersectional and intersubgeneric matings), mating success declines to some extent, but the number of successful "wide hybridizations" obtained in the experimental trials indicates that even the most morphologically and ecologically divergent of diploid *Erythrina* species have retained their ancestral chromosomal and genic homology and have not evolved substantial barriers to hybridization in concert with morphological differentiation. *Erythrina* forms a homogamic complex of interfertile species, or perhaps a series of homogamic complexes with weak to moderate barriers between the complexes. *Erythrina* shares this pattern of species relationships with many temperate-zone genera of trees and shrubs. The evidence from *Erythrina* suggests that the patterns of species relationships in predominantly or exclusively tropical groups of woody plants may not differ significantly from the patterns found in their better-known temperate-zone counterparts. Formation of homogamic complexes may be a common phenomenon in tropical woody plants and may be an important factor in the evolution of these taxa.

The patterns of inheritance of phenetic traits in the artificially produced hybrids (Section 5) confirm the true hybrid nature of these plants and demonstrate that matricliny, a potential complicating factor in the inheritance of these traits and in the interpretation of hybridization patterns, is not indicated in *Erythrina* hybrids. The patterns of inheritance in the artificial hybrids reveal the patterns to be expected in the detection and analysis of natural hybridization: for morphometric characters, a rather narrowly segregating array of intermediate types among the hybrids; and for discrete characters such as trichomes, possessed exclusively by either the female or male parent, the inheritance of the character in some of the hybrid offspring, the character being often reduced in size or density.

Evidence for the third hypothesis, concerning the pollination of sect. *Erythrina* by relatively specialized, widely foraging hummingbirds and the relation of this pollination system to *Erythrina* breeding systems, is presented in a separate paper (Neill, 1987). The pollination studies indicate that interspecific pollen flow and potential natural hybridization are likely to occur among sympatric species of sect. *Erythrina*.

Evidence for the fourth and fifth hypotheses, concerning natural hybridization and hybrid speciation in *Erythrina*, is presented in Section 6. Natural hybridization was detected among several co-occurring species of sect. *Erythrina* in Chiapas, Mexico, at the geographical center of diversity of the section. The natural hybrids display the same patterns of inheritance of phenetic traits as the artificial hybrids described earlier. The evidence for hybrid speciation itself is somewhat more equivocal. As stated in the introduction to this paper, the final hypothesis is historical and cannot be tested directly, but can be inferred only by drawing on information obtained by testing the first four.

The information presented throughout this paper does make plausible the hypothesis of hybrid speciation in *Erythrina*. Moreover, the research reported here provides a unique base of information for further studies of species relationships and the evolutionary history of *Erythrina*, as a model of evolutionary processes in flowering plants that may be common to many tropical woody genera. Perhaps the most incisive research that could be carried out at this point in the continuing biosystematic investigation of *Erythrina* would entail studies of isoenzymes and particularly of nucleic acid restriction sites among the taxa, as well as the inheritance of these molecular character states in the hybrids of known origin, followed by the construction of phylogenies combining molecular data with the presently available evidence on morphological and biogeographic patterns and the data from crossing experiments. The collection of *Erythrina* species and hybrids now available in cultivation at the

Hawaiian botanical gardens provides an ideal resource for such studies, and it is my hope that my colleagues specializing in chemosystematics and molecular phylogenetics do take advantage of this resource to investigate further the patterns of evolution in this interesting genus.

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APPENDIX I. *Species, sections, and subgenera of* Erythrina. *All recognized taxa in* Erythrina *are included in this list. I do not recognize infraspecific taxa in* Erythrina. *Proposed taxonomic changes are anticipated here, prior to their formal designation. The numbering sequence of Krukoff & Barneby (1974) is followed for reference to that work, and because the numbers were used to designate the hybrids. There are gaps in the number sequence because of reduction of species to synonymy. Species reduced to synonymy since Krukoff & Barneby (1974) are indicated at the end of this list.*

Erythrina L.

I. Subgenus *Micropteryx* (Walp.) F. G. Baker
- 1. Sect. *Duchassaingia* (Walp.) Krukoff
  - 1. *Erythrina fusca* Lour.
- 2. Sect. *Cristae-galli* Krukoff
  - 2. *Erythrina crista-galli* L.
  - 3. *Erythrina falcata* Benth.
- 3. Sect. *Micropteryx*
  - 4. *Erythrina dominguezii* Hassler
  - 5. *Erythrina ulei* Harms
  - 6. *Erythrina verna* Velloso
  - 7. *Erythrina poeppigiana* (Walp.) O. F. Cook

II. Subgenus *Erythrina*
- 4. Sect. *Suberosae* Krukoff
  - 8. *Erythrina suberosa* Roxb.
  - 9. *Erythrina microcarpa* Koord. & Valeton
  - 10. *Erythrina stricta* Roxb.
  - 11. *Erythrina resupinata* Roxb.
- 5. Sect. *Arborescentes* Krukoff
  - 12. *Erythrina arborescens* (Roxb.) Walp.
- 6. Sect. *Hypaphorus* (Hassk.) Krukoff
  - 13. *Erythrina subumbrans* (Hassk.) Merr.
- 7. Sect. *Breviflorae* Krukoff
  - 14. *Erythrina breviflora* A. DC.
  - 14a. *Erythrina petraea* Brandegee
  - 14b. *Erythrina oaxacana* (Krukoff) Krukoff
  - 14c. *Erythrina batolobium* Barneby & Krukoff
- 8. Sect. *Edules* Krukoff
  - 15. *Erythrina edulis* Triana ex M. Micheli
  - 15a. *Erythrina megistophylla* Diels
- 9. Sect. *Stenotropis* (Hassk.) Krukoff
  - 16. *Erythrina speciosa* Andrews
- 10. Sect. *Pseudo-edules* Krukoff & Barneby
  - 17. *Erythrina polychaeta* Harms
  - 18. *Erythrina schimpfii* Diels
- 11. Sect. *Leptorhizae* Krukoff
  - 19. *Erythrina montana* Standley

APPENDIX I. *Continued.*

- 20. *Erythrina leptorhiza* A. DC.
- 21. *Erythrina horrida* A. DC.
- 21a. *Erythrina sousae* Krukoff
- 12. Sect. *Erythrina*
  - 22. *Erythrina herbacea* L.
  - 23. *Erythrina standleyana* Krukoff
  - 24. *Erythrina flabelliformis* Kearney
  - 25. *Erythrina americana* Miller
  - 27. *Erythrina pudica* Krukoff & Barneby
  - 27a. *Erythrina krukoviana* Neill, sp. nov. ined.
  - 28. *Erythrina lanata* Rose
  - 29. *Erythrina goldmanii* Standley
  - 31. *Erythrina folkersii* Krukoff & Mold.
  - 32. *Erythrina tuxtlana* Krukoff & Barneby
  - 33. *Erythrina smithiana* Krukoff
  - 34. *Erythrina cochleata* Standley
  - 35. *Erythrina hondurensis* Standley
  - 36. *Erythrina chiapasana* Krukoff
  - 37. *Erythrina atitlanensis* Krukoff & Barneby
  - 38. *Erythrina cobanensis* Krukoff & Barneby
  - 39. *Erythrina williamsii* Krukoff & Barneby
  - 40. *Erythrina tajumulcensis* Krukoff & Barneby
  - 41. *Erythrina chiriquensis* Krukoff
  - 42. *Erythrina macrophylla* A. DC.
  - 43. *Erythrina guatemalensis* Krukoff
  - 44. *Erythrina globocalyx* Porsch & Cuf.
  - 45. *Erythrina steyermarkii* Krukoff & Barneby
  - 46. *Erythrina florenciae* Krukoff & Barneby
  - 47. *Erythrina berenices* Krukoff & Barneby
  - 48. *Erythrina huehuetenangensis* Krukoff & Barneby
  - 49. *Erythrina lanceolata* Standley
  - 50. *Erythrina costaricensis* M. Micheli
  - 51. *Erythrina barqueroana* Krukoff & Barneby
  - 53. *Erythrina berteroana* Urban
  - 54. *Erythrina rubrinervia* H.B.K.
  - 55. *Erythrina mexicana* Krukoff
  - 56. *Erythrina salviiflora* Krukoff & Barneby
  - 56a. *Erythrina santamartensis* Krukoff & Barneby
  - 57. *Erythrina castillejiflora* Krukoff & Barneby
  - 57a. *Erythrina thyrsiflora* Gómez & Gómez

APPENDIX I. *Continued.*

13. Sect. *Gibbosae* Krukoff & Barneby
    58. *Erythrina gibbosa* Cuf.
14. Sect. *Corallodendra* Krukoff
    59. *Erythrina amazonica* Krukoff
    60. *Erythrina similis* Krukoff
    61. *Erythrina peruviana* Krukoff
    62. *Erythrina mitis* Jacq.
    63. *Erythrina pallida* Britton & Rose
    64. *Erythrina corallodendrum* L.
    65. *Erythrina eggersii* Krukoff
    66. *Erythrina buchii* Urban
    67. *Erythrina leptopoda* Urban & Ekman

14a. Sect. *Fidelenses* Neill, sect. nov. ined.
    68. *Erythrina elenae* Howard & Briggs

15. Sect. *Cubenses* Krukoff
    69. *Erythrina cubensis* C. Wright

16. Sect. *Olivianae* Krukoff & Barneby
    70. *Erythrina oliviae* Krukoff

17. Sect. *Caffrae* Barneby & Krukoff
    71. *Erythrina caffra* Thunb.
    72. *Erythrina lysistemon* Hutchinson

18. Sect. *Humeanae* Barneby & Krukoff
    73. *Erythrina humeana* Sprengel
    74. *Erythrina zeyheri* Harvey

19. Sect. *Acanthocarpae* Barneby & Krukoff
    75. *Erythrina acanthocarpa* E. Meyer

III. Subgenus *Tripterolobus* Barneby & Krukoff

20. Sect. *Tripterolobus* Barneby & Krukoff
    76. *Erythrina greenwayi* Verdcourt

IV. Subgenus *Chirocalyx* (Meisner) Harvey

21. Sect. *Bruceanae* Barneby & Krukoff
    77. *Erythrina brucei* Schwein.

22. Sect. *Macrocymbium* (Walp.) Barneby & Krukoff
    78. *Erythrina vogelii* Hooker f.
    79. *Erythrina senegalensis* A. DC.

23. Sect. *Dilobochilus* Harms
    80. *Erythrina excelsa* Baker

24. Sect. *Dichilocraspedon* Harms
    81. *Erythrina mildbraedii* Harms

25. Sect. *Chirocalyx*
    82. *Erythrina pygmaea* Torre
    83. *Erythrina mendesii* Torre

APPENDIX I. *Continued.*

    84. *Erythrina baumii* Harms
    85. *Erythrina decora* Harms
    86. *Erythrina livingstoniana* Baker
    87. *Erythrina tholloniana* Hua
    88. *Erythrina addisoniae* Hutchinson & Dalziel
    89. *Erythrina droogmansiana* DeWild. & T. Durand
    90. *Erythrina orophila* Ghesq.
    91. *Erythrina sacleuxii* Hua
    92. *Erythrina haerdii* Verdc.
    93. *Erythrina sigmoidea* Hua
    94. *Erythrina latissima* E. Meyer
    95. *Erythrina abyssinica* Lam.

V. Subgenus *Erythraster* Barneby & Krukoff

26. Sect. *Erythraster*
    96. *Erythrina variegata* L.
    97. *Erythrina tahitensis* Nad.
    97a. *Erythrina sandwicensis* Degener
    98. *Erythrina euodiphylla* Hassk.
    99. *Erythrina vespertilio* Benth.
    100. *Erythrina merrilliana* Krukoff
    101. *Erythrina velutina* Willd.
    103. *Erythrina grisebachii* Urban
    104. *Erythrina burtii* Baker f.
    105. *Erythrina burana* R. Chiovenda
    106. *Erythrina perrieri* R. Viguier
    107. *Erythrina schliebenii* Harms ex Mildbr.
    108. *Erythrina melanacantha* Taubert ex Harms

Species reduced to synonymy since Krukoff & Barneby (1974):

Erythrina caribaea Krukoff & Barneby
= *E. berteroana* Urban × *E. folkersii* Krukoff & Mold.

Erythrina coralloides A. DC. = *E. americana* Miller

Erythrina insularis F. M. Bailey = *E. vespertilio* Benth.

The first two reductions to synonymy are proposed for the first time in this paper. The third reduction follows Krukoff's treatment in his post-1974 publications on *Erythrina*.

APPENDIX II. Erythrina *hybridization trials. This appendix summarizes the results of the interspecific hybridization trials for each species combination. For many of the species combinations, more than one accession was employed as the male and/or female parents. The identity of the individual parents is presented in Tables 11–13 only for the successful trials resulting in viable hybrid plants.*

The hybridization trials are grouped into five categories:

I. *Narrow hybridizations within sect.* Erythrina.
II. *Narrow hybridizations, excluding sect.* Erythrina.
III. *Intersectional hybridizations: female parent in sect.* Erythrina.
IV. *Intersectional hybridizations: male parent in sect.* Erythrina.
V. *Intersectional hybridizations: excluding sect.* Erythrina.

In categories III–V, the number in parentheses after the species name refers to the section to which the species belongs (see Table 1). An asterisk indicates a wide (intersubgeneric) hybridization.

Hybrid # = a number assigned to each hybrid combination, made up from the numbers assigned to the parental species as listed in Krukoff & Barneby (1974)
Pol = number of flowers hand-pollinated in the hybrid combination
Frt = number of pollinations producing mature fruits
Sds = total number of normal-sized seeds produced in the hybrid combination
Ger = number of seeds that germinated
Liv = surviving progeny; number of live F_1 plants in the hybrid combination

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
I. Narrow hybridizations within sect. *Erythrina*							
americana	*berteroana*	25×53	3	1	1	1	1
americana	*herbacea*	25×22	7	0	0	0	0
atitlanensis	*berteroana*	37×53	4	0	0	0	0
atitlanensis	*guatemalensis*	37×43	1	0	0	0	0
berteroana	*chiapasana*	36×53	4	0	0	0	0
berteroana	*folkersii*	53×31	14	0	0	0	0
berteroana	*guatemalensis*	53×43	21	1	8	6	6
berteroana	*rubrinervia*	53×54	3	0	0	0	0
berteroana	*salviiflora*	53×56	3	0	0	0	0
berteroana	*standleyana*	53×23	2	0	0	0	0
berteroana	*tajumulcensis*	53×40	4	0	0	0	0
chiapasana	*berteroana*	36×53	7	1	12	8	8
chiapasana	*folkersii*	36×31	1	0	0	0	0
chiapasana	*guatemalensis*	36×43	16	0	0	0	0
chiapasana	*macrophylla*	36×42	2	0	0	0	0
chiapasana	*tajumulcensis*	36×40	3	0	0	0	0
costaricensis	*berteroana*	50×53	12	0	0	0	0
folkersii	*berteroana*	31×53	22	0	0	0	0
folkersii	*guatemalensis*	31×43	5	0	0	0	0
goldmanii	*chiapasana*	29×53	12	1	1	1	1
guatemalensis	*berteroana*	43×53	13	4	25	14	8
guatemalensis	*chiapasana*	43×36	10	2	15	9	9
guatemalensis	*folkersii*	43×31	4	1	5	5	2
guatemalensis	*herbacea*	43×22	12	0	0	0	0
guatemalensis	*macrophylla*	43×42	7	4	17	12	8
guatemalensis	*salviiflora*	43×56	2	1	7	1	1
guatemalensis	*standleyana*	43×23	15	3	7	3	2
guatemalensis	*tajumulcensis*	43×40	23	6	17	9	9
herbacea	*americana*	22×25	2	2	4	3	3
herbacea	*berteroana*	22×53	14	2	3	1	1
herbacea	*chiapasana*	22×36	1	0	0	0	0
herbacea	*guatemalensis*	22×43	4	1	2	2	2
herbacea	*standleyana*	22×23	8	0	0	0	0
herbacea	*tajumulcensis*	22×40	2	0	0	0	0
macrophylla	*americana*	22×25	4	1	3	2	1
macrophylla	*atitlanensis*	42×37	1	0	0	0	0
macrophylla	*berteroana*	42×53	4	2	8	4	4

APPENDIX II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
macrophylla	*chiapasana*	42×36	6	1	3	0	0
macrophylla	*folkersii*	42×31	7	1	2	1	1
macrophylla	*guatemalensis*	42×43	17	2	6	4	4
macrophylla	*herbacea*	42×22	8	0	0	0	0
macrophylla	*salviiflora*	42×56	8	0	0	0	0
macrophylla	*standleyana*	42×23	2	0	0	0	0
macrophylla	*tajumulcensis*	42×40	9	1	1	0	0
rubrinervia	*berteroana*	54×53	2	0	0	0	0
salviiflora	*berteroana*	56×53	19	0	0	0	0
salviiflora	*guatemalensis*	56×43	3	0	0	0	0
standleyana	*berteroana*	23×53	19	0	0	0	0
standleyana	*guatemalensis*	23×43	8	0	0	0	0
standleyana	*herbacea*	23×22	10	0	0	0	0
tajumulcensis	*berteroana*	40×53	12	0	0	0	0
tajumulcensis	*guatemalensis*	40×43	8	1	4	4	4
tajumulcensis	*herbacea*	40×22	2	0	0	0	0
tajumulcensis	*macrophylla*	40×42	5	0	0	0	0
I. Total			417	39	142	90	75
II. Narrow (intrasectional) hybridizations: excluding sect. *Erythrina*							
		1. Sect. *Cristae-galli*					
crista-galli	*falcata*	2×3	22	2	4	1	1
falcata	*crista-galli*	3×2	14	4	7	0	0
		2. Sect. *Chirocalyx*					
abyssinica	*latissima*	95×94	3	1	2	1	1
abyssinica	*sacleuxii*	95×91	2	0	0	0	0
		3. Sect. *Erythraster*					
perrieri	*variegata*	106×96	10	4	12	10	9
sandwicensis	*variegata*	97a×96	8	0	0	0	0
tahitensis	*sandwicensis*	97×97a	7	0	0	0	0
tahitensis	*variegata*	97×96	26	0	0	0	0
tahitensis	*velutina*	97×102	19	0	0	0	0
variegata	*perrieri*	96×106	6	0	0	0	0
variegata	*vespertilio*	96×99	6	0	0	0	0
II. Total			123	11	25	12	11
III. Intersectional hybridizations: female parent in sect. *Erythrina*							
*berteroana**	*fusca* (1)	53×1	21	0	0	0	0
*chiapasana**	*fusca*	36×1	5	0	0	0	0
*folkersii**	*fusca*	31×1	8	0	0	0	0
*guatemalensis**	*fusca*	43×1	35	0	0	0	0
*herbacea**	*fusca*	22×1	10	1	4	4	4
*macrophylla**	*fusca*	42×1	10	1	3	0	0
*berteroana**	*crista-galli* (2)	53×2	2	0	0	0	0
*guatemalensis**	*crista-galli*	43×2	64	1	2	0	0
*herbacea**	*crista-galli*	22×2	10	0	0	0	0
*macrophylla**	*crista-galli*	42×2	20	0	0	0	0
*herbacea**	*dominguezii* (3)	22×4	3	0	0	0	0
guatemalensis	*stricta (4)*	43×10	5	0	0	0	0
guatemalensis	*arborescens* (5)	43×12	3	0	0	0	0
guatemalensis	*speciosa* (9)	43×16	10	0	0	0	0
herbacea	*speciosa*	22×16	2	0	0	0	0
macrophylla	*speciosa*	42×16	11	0	0	0	0
berteroana	*pallida* (14)	53×63	4	0	0	0	0

APPENDIX II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
guatemalensis	*amazonica (14)*	43×59	58	1	1	0	0
guatemalensis	*corallodendrum (14)*	43×64a	2	2	6	0	0
guatemalensis	*caffra* (17)	43×71	1	0	0	0	0
guatemalensis	*lysistemon (17)*	43×72	23	2	3	1	0
herbacea	*caffra*	22×71	2	0	0	0	0
guatemalensis	*humeana* (18)	43×73	5	1	1	0	0
herbacea	*humeana*	22×73	5	1	2	2	2
*guatemalensis**	*senegalensis* (22)	43×79	8	3	3	1	1
*guatemalensis**	*abyssinica* (25)	43×95	9	2	2	1	1
*guatemalensis**	*latissima* (25)	43×94	6	0	0	0	0
*macrophylla**	*abyssinica*	42×95	2	0	0	0	0
*macrophylla**	*latissima*	42×94	4	0	0	0	0
*guatemalensis**	*perrieri* (26)	43×106	12	0	0	0	0
*guatemalensis**	*sandwicensis (26)*	43×97a	25	0	0	0	0
*guatemalensis**	*variegata (26)*	43×96	26	0	0	0	0
*guatemalensis**	*vespertilio (26)*	43×99	4	1	2	0	0
*herbacea**	*perrieri*	22×106	8	0	0	0	0
*herbacea**	*variegata*	22×96	8	0	0	0	0
*macrophylla**	*sandwicensis*	42×97a	4	0	0	0	0
*macrophylla**	*variegata*	42×96	8	0	0	0	0
*macrophylla**	*vespertilio*	42×99	1	0	0	0	0
III. Total			444	16	29	9	8
IV. Intersectional hybridizations: male parent in sect. *Erythrina*							
fusca (1)*	*berteroana*	1×53	70	0	0	0	0
*fusca**	*folkersii*	1×31	8	0	0	0	0
*fusca**	*guatemalensis*	1×43	11	0	0	0	0
crista-galli (2)*	*guatemalensis*	2×43	10	4	15	10	8
stricta (4)	*guatemalensis*	10×43	6	0	0	0	0
arborescens (5)	*guatemalensis*	12×43	24	1	1	0	0
speciosa (9)	*berteroana*	16×53	3	0	0	0	0
corallodendrum (14)	*berteroana*	64×53	3	0	0	0	0
pallida (14)	*berteroana*	63×53	4	0	0	0	0
pallida (14)	*fusca*	63×1	2	0	0	0	0
humeana (18)	*berteroana*	73×53	3	0	0	0	0
abyssinica (25)*	*guatemalensis*	95×43	3	0	0	0	0
perrieri (26)*	*berteroana*	106×53	2	0	0	0	0
perrieri (26)*	*guatemalensis*	106×43	8	0	0	0	0
variegata (26)*	*guatemalensis*	96×43	7	0	0	0	0
variegata (26)*	*herbacea*	96×22	8	0	0	0	0
IV. Total			176	5	16	10	8
V. Intersectional hybridizations: excluding sect. *Erythrina*							
fusca (1)	*crista-galli* (2)	1×2	38	0	0	0	0
*fusca**	*lysistemon* (17)	1×72	1	0	0	0	0
*fusca**	*variegata* (26)	1×96	17	0	0	0	0
crista-galli (2)	*fusca* (1)	2×1	35	11	33	8	7
crista-galli	*dominguezii* (3)	2×4	34	0	0	0	0
*crista-galli**	*arborescens* (5)	2×12	1	0	0	0	0
*crista-galli**	*speciosa* (9)	2×16	14	2	2	2	1
*crista-galli**	*amazonica* (14)	2×59	18	1	1	0	0
*crista-galli**	*abyssinica* (25)	2×95	3	0	0	0	0
*crista-galli**	*perrieri* (26)	2×106	8	0	0	0	0
*crista-galli**	*sandwicensis* (26)	2×97a	5	2	3	0	0
*crista-galli**	*variegata* (26)	2×96	23	2	3	2	1
dominguezii (3)	*crista-galli* (2)	4×2	8	0	0	0	0

APPENDIX II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
arborescens (5)*	*crista-galli* (2)	12×2	15	1	1	0	0
arborescens	*humeana* (18)	12×73	7	0	0	0	0
*arborescens**	*sandwicensis* (26)	12×97a	15	0	0	0	0
speciosa (9)*	*fusca* (1)	16×1	3	0	0	0	0
*speciosa**	*crista-galli* (2)	16×2	33	0	0	0	0
speciosa	*lysistemon* (17)	16×72	64	3	7	4	4
caffra (17)*	*fusca* (1)	71×1	5	1	2	2	2
lysistemon (17)*	*fusca* (1)	72×1	10	0	0	0	0
lysistemon	*speciosa* (9)	72×16	46	3	8	4	3
*lysistemon**	*abyssinica* (25)	72×95	11	0	0	0	0
*lysistemon**	*latissima* (25)	72×94	4	0	0	0	0
senegalensis (22)*	*fusca* (1)	79×1	8	0	0	0	0
abyssinica (25)*	*fusca* (1)	95×1	5	0	0	0	0
*abyssinica**	*crista-galli* (2)	95×2	2	0	0	0	0
*abyssinica**	*humeana* (18)	95×73	5	1	1	0	0
*abyssinica**	*sandwicensis* (26)	95×97a	1	0	0	0	0
*abyssinica**	*variegata* (26)	95×96	1	0	0	0	0
latissima (25)*	*lysistemon* (17)	94×72	16	0	0	0	0
*latissima**	*humeana* (18)	95×73	5	0	0	0	0
perrieri (26)*	*fusca* (1)	106×1	3	0	0	0	0
variegata (26)*	*fusca* (1)	96×1	32	0	0	0	0
*variegata**	*crista-galli* (2)	96×2	2	0	0	0	0
*variegata**	*speciosa* (9)	96×16	6	0	0	0	0
*variegata**	*senegalensis* (22)	96×79	7	0	0	0	0
V. Total			511	27	61	22	18

APPENDIX III. *Sources of cultivated* Erythrina *used as parentals in successful interspecific hybridizations. (W): Accession obtained from known wild populations; (NW): Accession obtained from cultivated source, or otherwise not from a known wild population.*

Vouchers (from plants cultivated in Hawaiian gardens) are deposited at MO. Location of voucher from original wild collection of seed is indicated here if known.

Erythrina abyssinica Lam. PT 770034001
Kenya: Nairobi. *E. Taylor 17.* (NW)

Erythrina abyssinica Lam. PT 731006002
Kenya: Nairobi, cultivated tree in yard of Cunningham van Someren. (NW)

Erythrina americana Miller WA 75c1171
Mexico: Mexico City, cultivated tree. *L. S. Ayres s.n.* (Waimea received as cutting from Los Angeles State & County Arboretum # 565874) (NW)

Erythrina berteroana Urban PT 730311001
Guatemala: Suchitepequez. Nahualate, Finca El Salvador. *B. A. Krukoff 1973-13* (NY). (W)

Erythrina berteroana Urban PT 700044001, -002
Panama: Canal Zone. Tree cultivated at Summit Gardens. *W. S. Stewart s.n.* (NW)

Erythrina berteroana Urban WA 74s864
Guatemala: Suchitepequez. Municipio Chicacao. *B. A. Krukoff 1968-508* (NY). (W)

Erythrina berteroana Urban WA 78s564
Panama: Canal Zone. Between Madden Dam and Chilibre. *J. Folson 3661* (MO). (W)

Erythrina caffra Thunb. WA 74c1456
South Africa: Cape Province, Grahamstown, elev. 2,400 ft. *Roy Bayliss s.n.* (Waimea received as cutting from Foster Garden # 69.265) (W)

Erythrina chiapasana Krukoff PT 721005001
Guatemala: Huehuetenango, near La Estancia. *B. A. Krukoff 1969-68* (NY). (W)

Erythrina chiapasana Krukoff PT 730710001
Guatemala: Huehuetenango, near La Estancia. *B. A. Krukoff 1973-16* (NY). (W)

Erythrina crista-galli L. PT 740283001
Paraguay: near Asunción. *Conrad & Die 2191.* (W)

Erythrina crista-galli L. WA 74p840
South Africa. Cultivated tree; seed received from Wm. J. Tijmens, Univ. of Stellenbosch. (Waimea received as live plant from PT 72s352) (NW)

Erythrina falcata Benth. PT 750086001
Argentina. Thays Botanical Garden, cultivated tree. *E. Pingitore s.n.* (NW)

Erythrina folkersii Krukoff & Mold. PT 700010001
Guatemala: Izabal, at junction of road to Puerto Barrios and Mathias Calves. *B. A. Krukoff 1969-109* (NY). (W)

Erythrina fusca Lour. PT 740230005, WA 74599
Guatemala: Escuintla. *B. A. Krukoff 1972-12* (NY). (W)

Erythrina guatemalensis PT 700018001, WA 74c1453
Guatemala: Alta Verapaz, along Cobán–Salama road, near Santa Cruz, elev. 1,280 m. *B. A. Krukoff 1969-195* (NY). (W) Note: The tree at Waimea Arboretum WA 74c1453 was grown from a cutting taken from PT 700018001, so the two accessions are genetically identical.

Erythrina guatemalensis Krukoff PT 720999002
Guatemala: Huehuetenango, near Barillas. *B. A. Krukoff 1969-200* (NY). (W)

Erythrina guatemalensis Krukoff PT 750419001
Guatemala: Huehuetenango, near Barillas. *B. A. Krukoff s.n.* (W)

Erythrina herbacea L. PT 75c1103
California: Los Angeles State & County Arboretum # 54s1201, cultivated. (NW)

Erythrina herbacea L. WA 76s187
Florida: Miami, Fairchild Garden, cultivated. (NW)

Erythrina humeana Sprengel WA 74p1382
South Africa: locality unknown. *D. Millington s.n.* (NW)

Erythrina latissima E. Meyer PT 750281004
South Africa: Natal. Cultivated tree at Pine Town Gardens. *Ian Whitton 750401.* (NW)

Erythrina lysistemon Hutchinson PT 750280002, -003
South Africa: Natal, Durban. *Ian Whitten s.n.* (1975) (W)

Erythrina macrophylla A. DC. PT 750420002, WA 75s1136
Guatemala: Sololá, near Godinez. Elev. 6,145 ft. *B. A. Krukoff 1975-4* (NY). (W)

APPENDIX III. *Continued.*

Erythrina perrieri R. Viguier WA 74s857
Madagascar: Maintirano, near Bekopaka. *Fred Meyer s.n.* (W)

Erythrina salviiflora Krukoff & Barneby PT 721000002
Guatemala: Suchitepequez, Municipio Chicacao, Finca El Naranjo. Elev. 1,070 m. *B. A. Krukoff 1969-58* (NY). (W)

Erythrina senegalensis A. DC. WA 74s100
Nigeria: Coastal area. Seeds received from B. A. Krukoff; collector unknown. (W)

Erythrina speciosa Andrews PT 730708001, PT 730742002
Brazil: São Paulo. Cultivated tree at São Paulo Botanical Garden. *B. A. Krukoff 1973-20* (NY). (NW)

Erythrina standleyana Krukoff WA 76s1056
California: Escondido. Cultivated tree. (NW) Originally collected as seed by Fred Meyer from wild tree, Yucatán, Mexico.

Erythrina tajumulcensis Krukoff & Barneby WA 74c1448
Guatemala: San Marcos, near Aldea Feria, along road from San Marcos to San Rafael de La Costa. *B. A. Krukoff 1969-249* (NY). (Waimea received as cutting from PT 700015001) (W)

Erythrina variegata L. WA 74s892
Hawaii: Honolulu, Mid-Pacific Country Club, cultivated (white-flowered form). *Beatrice Krauss s.n.* (NW)

Erythrina variegata L. WA 76s996
Mariana Islands: Saipan Unai, Laulau Beach. *Derral Herbst s.n.* (W)